VOLUME XXXV NUMBER 4

BOTANICAL GAZETTE

APRIL, 1903

OOGENESIS IN SAPROLEGNIA.[1]

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. XLVI.

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(WITH PLATES IX AND X)

ALTHOUGH Saprolegnia is a form of considerable interest in connection with the problem of the so-called multinucleate gametes, nevertheless investigations have not been carried forward upon it with that attention to cytological detail that has recently been given to other Phycomycetes, *e. g.*, Albugo, Peronospora, Pythium, and Sclerospora.

The present paper deals chiefly with the events of oogenesis and a comparison of this process with the development of zoospores. The material employed was apogamous, indeed apandrous, for specimens were chosen entirely free from antheridia to the end that the investigation might be relieved from the dispute on the sexuality of these fungi. However, as will be seen, the results have an important bearing on the well-known binucleate eggs, assumed by Trow to be stages of fertilization. At the end of the paper will be found an account, entitled "Theoretical Considerations," which deals with a number of topics suggested by this study in relation to recent investigations upon Phycomycetes and Ascomycetes.

The material was isolated in pure cultures and cultivated for several months on various substrata, during which time the writer had the opportunity of observing and confirming many of

[1] Published also in Decennial Publications, the University of Chicago, I. 10 : 225–257. *pls. 15, 16.* 1903.

the adaptations recorded by Klebs (1899) in his detailed study of *Saprolegnia mixta*. In this period a number of structural peculiarities appeared, associated with the various sorts of nutrition, and forms arose presenting the characters of three closely related species, *Saprolegnia mixta*, *S. monoica*, and *S. ferax*. The variation was most marked in respect to the presence, absence, or relative quantity of antheridia which are the most important distinguishing marks of these species.

The original collection bore oogonia with relatively few antheridia (*Saprolegnia mixta*), and frequently none. By cultivating the form on a rich substratum—raw beef or fresh insects—a much more extensive growth of antheridial filaments was obtained, as in *Saprolegnia monoica*. On other media—boiled whites and yolks of eggs and dried beef—the filaments never produced antheridia, but oogonia were formed abundantly (as in *Saprolegnia ferax*), normal in size and with numerous oospores. After three months all cultures ceased to develop antheridia and the number of oogonia steadily decreased until the cultures reproduced entirely by zoospores. It was always possible to get oospores, as Klebs (1899) has shown, by placing cultures developing zoosporangia under such conditions that the hyphae were no longer submerged. This may readily be done by removing material from water and placing it in a dish of cold agar-agar, which will furnish enough moisture to support the fungus for several weeks. The filaments out of water promptly developed oogonia, even when they had the form characteristic of zoosporangia. Such cultures frequently showed club-shaped oogonia whose eggs were arranged approximately in a line.

Chromacetic acid proved to be the most satisfactory fixing agent, but it must be employed much weaker than the usual formula. One per cent. chromacetic acid caused immediate contraction of the protoplasm, but a solution one-fourth per cent. chromic and one-tenth per cent. acetic acid gave excellent results, and presented advantages of clearness and preservation over weak Flemming, Merkel, corrosive sublimate, sublimate acetic, iridium chlorid, or picric acid. Paraffin sections were cut 3–5 μ thick, and generally stained with safranin and gentian

violet. The protoplasmic structures are so minute as to require lenses of the clearest definition, and the Zeiss apochromatic objectives 2^{mm} and 1.5^{mm} with the compensating oculars were employed throughout the investigation.

OOGENESIS.

The accounts of nuclear and cytoplasmic activities in Saprolegnia during oogenesis present some striking contradictions, and leave untouched some phases of a detailed but very significant character. Humphrey (1892) was the first author to apply methods of cytological technique, cutting sections in paraffin, and his studies were followed by the investigations of Trow (1895, 1899) and Hartog (1895, 1896, 1899). The last two authors have expressed very divergent views, asserted with a positiveness that invests their discussions with an atmosphere of personal criticism that need not be reviewed in this paper. It is necessary, however, to consider certain conclusions of the earlier authors with which the present writer is not in accord, and it seems best to do this at the outset, leaving the points of agreement with the present investigation to be taken up in their proper connections.

It is well known that the oogonium of the Saprolegniales contains many times more nuclei than the number of eggs ultimately formed. Humphrey and Hartog believed that the nuclei fused with one another, thus reducing the sum total until the requisite number was present. Trow stated that the number was diminished through degeneration and digestion until it was so small that each egg took but a single nucleus. The writer has found no evidence of nuclear fusions as reported by Humphrey and Hartog, and in general supports Trow's view of degeneration. However, there seems to be a reason, not known to Trow, for the selection of the fortunate nuclei destined to preside over the eggs, and a large part of this paper will deal with that subject.

It is also well known that the eggs of the Saprolegniales are not infrequently binucleate, and sometimes trinucleate. Humphrey and Hartog considered such conditions as merely the final

stages in the process of general nuclear fusion, the last pairings whereby the eggs become uninucleate. Trow has made much of these binucleate eggs, believing the two nuclei to be sexual and one of them introduced by an antheridial filament. He has been bold enough to assert sexuality for four members of the group: *Saprolegnia declina*, *S. mixta*, *Achlya americana*, and *A. americana cambrica*. Nevertheless, Trow presents very little evidence that the so-called "male" nucleus comes from the antheridial tube, or that the latter structure ever opens into the eggs. The writer cannot justify Trow's conclusions in this matter, believing them premature as to evidence and illogical as to probabilities. The present study will attempt to show that binucleate and trinucleate eggs are to be expected under the peculiar conditions governing oogenesis.

With respect to cytological details, investigations scattered over so long a period as twelve years could hardly be expected to agree. Hartog studied from entire mounts, yet was able to count chromosomes and observe nuclear figures. Trow sectioned in paraffin, and was at first (1895) completely deceived as to the interior structure of the nucleus and the number of chromosomes. In his second paper, however, Trow (1899) concedes that the nuclei in the antheridia and oogonia divide mitotically, but his figures are far from clear as to detail. Trow was also mistaken in his interpretation of the nucleolus.

The present study will give a more detailed account of nuclear structure and activities than any previous paper. But the most important contribution relates to certain cytoplasmic manifestations that seem to determine in large part the results of oogenesis. These cytoplasmic activities place the process of oogenesis in Saprolegnia in a new light, bringing it into sympathy with conditions in Albugo, Peronospora, and Sclerospora. They are concerned with that cytoplasmic structure termed the coenocentrum.

It is not strange that Humphrey, Hartog, and Trow failed to find the coenocentrum, for its recognition demands exceptionally good fixation and staining. It is probable that Dangeard saw it when he described an oil globule or fatty mass in the cen-

ter of the egg. It seems possible that Trow may have mistaken it at times for a centrally placed nucleus, to which it bears a certain resemblance that might make the two structures indistinguishable in obscurely stained preparations. The coenocentrum does not appear until the processes of oogenesis are well under way. Previous to this period there are nuclear and cytoplasmic activities of considerable import, and they will be considered first.

It is well known that with the flow of the protoplasm into the swollen tip of a hypha there is apparent that peculiar structure of the protoplasm (*fig. 1*), significant of its streaming movement. The nuclei at that time are very small. When the oogonium is cut off by a septum from the hypha that bears it, the protoplasm becomes distributed almost homogeneously through the interior (*fig. 2*). The nuclei then increase in size, and shortly after show most clearly that detail of structure that is to be expected in the resting nucleus. This structure agrees with the accounts of Harper, Wager, Stevens, and myself for the nuclei in other types of fungi, indicating that the conditions among these lower forms are essentially similar to the nuclear structure of higher plants. As is shown in *figs. 3* and *4*, and especially in *fig. 6*, there is a nuclear membrane inclosing a well-differentiated nucleolus, prominent by its size and staining qualities. Much less conspicuous, but readily demonstrated in well-fixed material, is a loose linin network which contains the chromatic material. Trow's description of a central body containing chromatin and nucleolar matter, but "neither a nucleolus nor a chromosome," must have been founded on inferior preparations. There are certainly no complexities in Saprolegnia comparable to the so-called nucleolus of Spirogyra (Mitzkewitsch, 1898, Wisselingh, 1900).

There is one mitosis in the oogonium, but previous to that event a number of vacuoles are developed which generally result in a peripheral arrangement of the protoplasm around a large central space or vacuole containing cell sap. The vacuoles begin to appear immediately after the oogonium is cut off from the parent hypha (*fig. 2*). They grow larger and run together as bubbles do in soapsuds (*fig. 3*), until finally there are one or

perhaps two large vacuoles in the center, and occasionally smaller ones near the edge (*figs. 10, 11*). The protoplasm then lies as a thick peripheral zone, and the nuclei (*fig. 5*) are distributed at varying distances between the oogonial wall and the boundary of the vacuole.

This is the period when one may expect to find the nuclei in mitosis. This event happens to most nuclei at about the same time, and good preparations of this stage of oogenesis are very striking (*fig. 5*). The oogonium is filled with the diamond-shaped spindles inclosed in nuclear membranes. Three stages of mitosis are shown in *figs. 7–9*. It will be noted that the spindle is intranuclear. *Fig. 7* presents the condition just previous to metaphase, with the chromosomes, four in number, at the nuclear plate and the nucleolus lying outside of the spindle. *Fig. 8* is of a stage shortly after metaphase, when the two sets of daughter chromosomes have separated and are about to pass to the poles; the nucleolus is still present, but smaller and staining faintly. *Fig. 9* is of anaphase, the two groups of daughter chromosomes, four in each, lying at the poles of the spindle and the nuclear membrane manifestly about to disappear. The nucleolus probably dissolves; at least I have never been able to follow it much beyond metaphase, but surviving it would of course soon be lost in the granular cytoplasm after the breaking down of the nuclear membrane. Although granules are sometimes present at the poles of the spindles, the latter are generally entirely free from appearances that might suggest centrosomes.

It will be noted that this description of mitosis in Saprolegnia is similar in all essentials to the accounts of Wager (1896), Stevens (1899, 1901), and myself (1900) for Albugo; Wager (1900) for Peronospora; Miyake (1901) and Trow (1901) for Pythium; and Stevens (1902) for Sclerospora. The studies cover a wide range of forms and material. They agree in describing the spindle as always intranuclear and without centrosomes. The nucleolus is a structure always distinct from chromatic material and always, so far as we know, disappearing during mitosis by dissolution or extrusion into the cytoplasm. The chromosomes are derived from a linin network, and after mitosis

the chromatin returns to the granular condition generally present in resting nuclei.

Following mitosis, the oogonium passes into a condition that is exceedingly difficult to study. The number of nuclei has been doubled by the division, but the daughter nuclei are much smaller than the parents. A comparison of *fig. 4* with *fig. 10* will illustrate well the change. It is not the small size, however, that makes the examination so difficult, but the fact that these nuclei very shortly show signs of degeneration. Almost all of the nuclei are affected. The nuclear membrane becomes indistinct, and its contents finally lie as granular matter in a clear area that resembles, and probably is, a vacuole. The granular matter is undoubtedly derived in large part from the nucleolus that fragments, but some of it may be chromatin. The study of the steps in this process of general degeneration is especially baffling because the progress is toward a time when the nuclear material becomes indistinguishable from other granules in the cytoplasm.

It is difficult to understand how Humphrey and Hartog could ever have interpreted this process of degeneration as successive nuclear fusions. As Trow pointed out, successive fusions should give more and more conspicuous nuclei, as the material accumulated with each union, and consequently an ever-increasing clearness of conditions. In reality, however, we pass from the stage illustrated by *fig. 10* just after mitosis, to the vague conditions presented in *figs. 11*, *14*, and *15*. The last two figures are of oogonia much older than those shown in *figs. 10* and *11*, and illustrate late stages in the process, when the nuclear membranes have mostly disappeared and the nucleoli and possibly chromatic material lie in vacuoles. Such vacuoles are frequently elongated, and when they contain two masses of deeply staining material there is suggested a stage in nuclear fusion, and such appearances probably deceived Humphrey and Hartog. However, the vagueness of structure and manifest waning of the previous clear definition should have put these observers on their guard. These degenerate nuclei remain for a long time, even after the eggs are fully formed, and it is quite impossible to tell with exactness when they lose their structure and functions.

The eggs are formed during the process of nuclear degeneration described above, and their nuclear structure is really determined by that event. Trow (1899) has given a very good account of the general stages in this process of protoplasmic segmentation, but he did not know the cytological details, and there is reason to believe that he may have been mistaken in his interpretation of certain structures which he considered nuclei. The first external indication of protoplasmic segmentation is the gathering of the contents of the oogonium into denser masses around certain centers, these masses projecting into the central vacuole and destroying that even outline present in earlier conditions of the oogonium (*fig. 5*). The protoplasm between the egg origins is less dense, and presently begins to develop small vacuoles (*fig. 12*), which run together until the egg origins are separated by spaces of considerable size (*fig. 13*). Many of these vacuoles break through the films of protoplasm into the central space, which then appears to have put out extensions toward the cell wall. The protoplasm of the oogonium is exceptionally mobile at this time, and the vacuoles are constantly changing their form and position. In the end the protoplasm gathers more and more closely around the centers of the spore origins, and finally the latter break away from one another at all points of mutual contact (*fig. 13*), and the several independent protoplasmic masses round themselves off as eggs.

The reader will have noticed in the illustrations of this protoplasmic segmentation that each egg origin has a deeply stained center surrounded by delicate rays (*figs. 12–15*). These star-like structures are very conspicuous under low magnification (in *figs. 12* and *13*, 500 diameters), when the center appears to be a single structure. In reality it is not a simple unit, but is always composed of at least two structures, a coenocentrum accompanied by a nucleus. This dual nature is made clear only under high magnification, with clear preparations of very thin sections. I do not think it would be possible to understand the structure from entire mounts such as Hartog's. Hartog probably considered the center as a nucleus alone, and certain of Trow's figures indicate that he gave a similar interpretation. The coenocen-

trum is really the key to many of the problems of oogenesis in Saprolegnia.

The coenocentrum varies in its minute structure with different periods of oogenesis. It is at first a small body composed of several granules imbedded in dense material, from which a number of delicate fibrils radiate into the surrounding cytoplasm. The structure stains deeply and resembles an aster. After the eggs are fully formed the rays disappear and the coenocentrum grows larger, takes on a spherical form, and resembles a globule of oil or fat. It finally dissolves, sometimes with fragmentation, and completely disappears, in the older eggs. The coenocentrum is thus a structure peculiar to that period of oogenesis characterized by nuclear degeneration and the segmentation of the protoplasm to form the eggs. It bears a most important relation to these two events, which are the most difficult to study in the entire process of oogenesis.

We must begin with the first appearance of the coenocentra. These structures may always be found before the differentiation of the egg origins, at the time when the oogonium is filled with degenerating nuclei. The latter lie scattered through the cytoplasm (*figs. 14, 15*), and exhibit varying degress of dissolution. The young coenocentra are always found in the densest regions of the protoplasm, portions destined to become egg origins, such as are shown in *figs. 14* and *15*. They are very small at first and would scarcely be noticed except for the radiating fibrils that mark their position. They increase in size as the egg origins take more definite form (*fig. 16*).

An examination of *figs. 14–16* shows at the side of each coenocentrum a small nucleus. This structure is very small at early periods of oogenesis (*figs. 14, 15*), and scarcely more clear than many of the degenerating nuclei in the neighborhood; but as oogenesis proceeds the nucleus accompanying the coenocentrum grows larger and increases greatly in staining material (*fig. 16*). When the eggs are fully formed, this nucleus is many times larger than at the first appearance of the coenocentrum, as may be seen by comparing *figs. 17–21* with *figs. 14* and *15*, which are all magnified 1,000 diameters. One would hardly think it

possible that the large nucleus present in the center of the mature egg was ever so small as the degenerating nuclei whose remains may be found in advanced stages of oogenesis (*fig. 16*), and sometimes even in the fully formed eggs (*figs. 17* and *23*); but there seems to be no doubt of this. The nucleus destined to preside over the egg is at first indistinguishable in size or structure from many of its neighbors. What should lead to its selection as the egg nucleus? I can see no other explanation than that its position gives it dynamic advantages, enabling it to survive when its neighbors lack the metabolic conditions necessary for nuclei and consequently must degenerate. This conceives the oogonium as too richly stocked with nuclei for the metabolic conditions of oogenesis, and in consequence the field of a struggle of the parts ("der Kampf der Theile," Roux).

What is the relation of the coenocentrum to these events? As we have stated, the coenocentrum is not a permanent organ either in the oogonium or the egg. It appears with the first indications of the egg origins and passes away as the eggs grow older. It is obviously a transitory structure peculiar to the most active periods of oogenesis. To the writer the coenocentrum seems to be the morphological expression of dynamic activities in the oogonium, and especially in the egg origins at the time when these are differentiated. It has the appearance of being the focal point in the center of the egg origins of the metabolic conditions peculiar to oogenesis; and this offers a very plausible explanation of the survival of the nucleus which lies nearest the coenocentrum.

The nucleus most fortunate in its position near the coenocentrum should be greatly benefited if this is a region of the protoplasm more favorably nourished than other parts. It is probable that the coenocentrum even draws toward itself nuclei within a certain sphere of attraction. Nuclei may be found with a pointed end extended toward the coenocentrum (*figs. 16, 20*). It will be remembered that Stevens (1901) showed with great clearness for *Albugo candida* and *A. Tragopogonis* that the nuclei in the immature eggs stretch toward the coenocentra so that their long dimensions are frequently twice the width. The nuclei of

Saprolegnia are too small to present conspicuous morphological evidence of this character; but we have the fact that the favored nucleus is almost always pressed against the coenocentrum which, together with the appearance of the nuclei and what we know of the events in Albugo, makes it quite certain that the coenocentrum exerts a chemotactic influence.

The changes that come over the egg as it matures are illustrated in *figs. 16–21*, which show the usual uninucleate condition of the egg. Binucleate and trinucleate eggs will be described in the following paragraphs. The two most important events of maturation are the increase in size of the nucleus and the gradual dissolution and final disappearance of the coenocentrum. The growth of the nucleus involves not only the extent of the space inclosed in the nuclear membrane (*figs. 17–21*), but also means a great increase in the amount of staining material, chromatic and nucleolar. The latter must be very many times greater in quantity in old eggs than at the beginning of oogenesis (compare *fig. 16* with *figs. 20* and *21*). The coencentrum decreases in size until it becomes a very small globule (*fig. 20*), or it may split up into several granules, which soon become lost in an ill-defined mass of denser protoplasm. The coenocentrum finally disappears, and the contents of the egg then arrange themselves around a central vacuole, with the nucleus taking a peripheral position. This is the structure of the mature egg, and is illustrated in *fig. 21*.

We will now consider some conditions that have given rise to much discussion, namely, the binucleate and trinucleate eggs. They have been found by Humphrey, Hartog, and Trow, and the present study indicates that they may be expected in any member of the Saprolegniales. Trow attached much significance to them as evidence of sexuality, but his conclusions seem to the writer open to much criticism and will be taken up later. *Figs. 22–25* illustrate several conditions that show how easily an egg may become binucleate. Suppose two nuclei lie near enough to the coenocentrum to share about equally the advantages of position. Then it is not likely that either will give way to the other. Such conditions in a young egg are shown in *fig. 22*.

Fig. 25 also represents a pair of nuclei one above the other and both extended toward the coenocentrum, which was fast breaking down. *Fig. 24* is very interesting. In this instance the coenocentrum is the center of a mass of protoplasm considerably larger than the average egg. There are two well-developed nuclei, and the form of the cell suggests the probability that material which ordinarily would have gone into two egg origins has been held together in this instance by the influence of an especially large coenocentrum. An illustration of quite the reverse condition is shown in *fig. 23*, and is remarkable. Here we have presented an egg with two coenocentra, and at the side of each a nucleus. There is no doubt from the age of the eggs that the two nuclei in each of these cases are sister nuclei. It is plain that the processes that work for the segmentation of the protoplasm in the oogonium are complex, not all in the influence of the coenocentrum, nor yet all in the general activities of the cytoplasm.

Give the egg two nuclei with a fair start over their degenerating neighbors, and they seem to be able to exist side by side, not differing, so far as one may see, from the nuclei of uninucleate eggs. The two nuclei may lie far apart, as in *fig. 26*, or so near together that they touch, as in *figs. 25* and *27;* but in no instance—and I have seen a great many binucleate eggs—have I ever observed them fusing. Trow (1899) reported an instance of nuclear fusion in the egg, but the writer thinks we are justified in waiting for confirmation of this observation before attaching to it the importance given by that author.

Trinucleate eggs are somewhat rare in *Saprolegnia mixta*. I have seen hardly more than a dozen, and these were all rather mature examples. I have never been fortunate enough to find young stages, periods comparable to *figs. 22–24* of the binucleate eggs. The three nuclei may be grouped close together in the egg (*fig. 28*), or may lie quite separate from one another (*fig. 29*). There is no evidence that they fuse. The rather meager data at hand indicate that when there are three nuclei in an egg they are individually smaller than the single nucleus in an ordinary egg (compare *figs. 28* and *29* with *figs. 19–21*). This is to be

expected, for in general the three nuclei share between them the metabolic possibilities of about the same amount of protoplasm as is in the uninucleate egg. The trinucleate egg probably develops, as does the binucleate, from an egg origin in which more than one nucleus by fortunate position is able to survive the processes of general degeneration.

Let us now examine Trow's position respecting sexuality in the Saprolegniales. It is presented most completely in his 1899 paper. I approach this subject with some diffidence, for it has already been the occasion of detailed discussions of a personal character (Hartog, 1896, 1899). The matter is finally reducible to a question of confidence in Trow's evidence, his account, and his figures. Everyone must admit the possibility of sexuality in the Saprolegniales, but the question for us is, does Trow prove it?

The binucleate egg gave Trow the conviction, as he acknowledges, that fertilization took place through the introduction of a male nucleus into the egg from an antheridial tube. But the present studies show that binucleate eggs are quite common in an undoubted apogamous form, the material being entirely free from antheridial filaments. Moreover, these binucleate eggs have been followed through younger stages back almost to the period of the egg origins, and we know that these two nuclei were sisters in the oogonium. To make this point more plain, let the reader contrast the appearance of the two small nuclei shown in *figs. 22* and *23* with the nuclei in older eggs (*figs. 19–21*), and it will be evident that the former have the size and structure of nuclei in the young oogonium, and not of the fully mature gamete (egg) nucleus. It should also be noted that Hartog's binucleate eggs were also from apogamous material (Hartog, 1898 and 1899, p. 450).

If, then, apogamous material may have binucleate eggs, and the events of oogenesis explain the conditions, we are justified in examining Trow's evidence of sexuality very critically and demanding of it exceptional fulness and accuracy. We are concerned chiefly with Trow's figures, for they should show most exactly what the investigator really saw. I have been impressed

with the lack of detail in many of these figures, which has led me to think that Trow may have made a number of mistakes which would quite invalidate his evidence in support of sexuality. *Figs. 43, 44,* and *46,* labeled "female gameto-nuclei," give appearances which are very similar to coenocentra, and I fear that he was not able to separate these structures in his preparations. *Fig. 35* certainly indicates that his material had coenocentra. But the most serious difficulties are encountered in his drawings of male gameto-nuclei (*figs. 45, 46*). These are not clear enough to be convincing; indeed, they seem to the writer to be the remains of degenerating nuclei at the periphery of the egg. Side by side with the structures labeled "male gameto-nuclei" Trow figures bodies, very similar in appearance, which are probably degenerate nuclei. In the face of this uncertainty and seeming contradiction of evidence the illustration of an antheridial filament piercing the egg (Trow, 1899, *fig. 45*) loses much of its weight, and the statement that two nuclei fuse in the center of the egg (Trow, 1899, *fig. 47*) is open to much doubt. The subject is so difficult that there are abundant opportunities for error, and we are justified in asking for much more evidence before accepting such important conclusions.

The writer cannot better sum up his attitude toward Trow's opinions on sexuality in the Saprolegniales than by defining them as *not proven* and *improbable* in the face of the mass of observations upon which botanists have generally agreed that the group is apogamous. The view of apogamy formerly resting entirely on the failure to find antheridial tubes fusing with the eggs is now supported by the present investigation on the details of oogenesis. These show that the binucleate egg, formerly difficult to understand on the theory of apogamy, may arise very naturally in a multinucleate oogonium when the method of oogenesis is as just described for *Saprolegnia mixta.*

The binucleate and trinucleate eggs of Saprolegnia are essentially similar to the multinucleate eggs of *Albugo Bliti* and *A. Portulacae,* and the conditions in the young eggs of *A. candida* and *A. Tragopogonis,* as described by Stevens (1899–1901). The latter, it will be remembered, contain several

potential gamete nuclei, but, so far as we know, only one of these becomes functional. But it would not be surprising to find at any time binucleate or trinucleate eggs among species of Albugo that are normally uninucleate.

In concluding, we must lay emphasis upon the importance of the coenocentrum as an index of the activities peculiar to oogenesis in Albugo, Peronospora, Sclerospora, Pythium, and Saprolegnia. Although this structure is probably in large part the expression of activities of the protoplasm as a whole, still there can be no doubt of its material existence. It is difficult to understand how Trow (1901, p. 291) can question this point, except that his figures indicate that fine details of structure were not shown in his preparations.

It would be strange, indeed, if so large a mass of protoplasm as the coenocentrum should not react in turn on the protoplasm that gave it birth. The coenocentrum is not a mass of food material, even though much of its granular substance may be the products of metabolism, and the structure as a whole trophoplasmic in character. It is protoplasm, and as such must be counted a factor in the subtle processes of oogenesis. Trow's comparison of the coenocentrum to a whirlpool in a river is not good, for there is unquestionably in this structure the expression of chemical phenomena as well as physical. The evidence is very strong from Stevens's (1901) work on Albugo, and the present study on Saprolegnia, that the coenocentrum has a sphere of chemotactic influence on the nuclei in its neighborhood.

SPOROGENESIS.

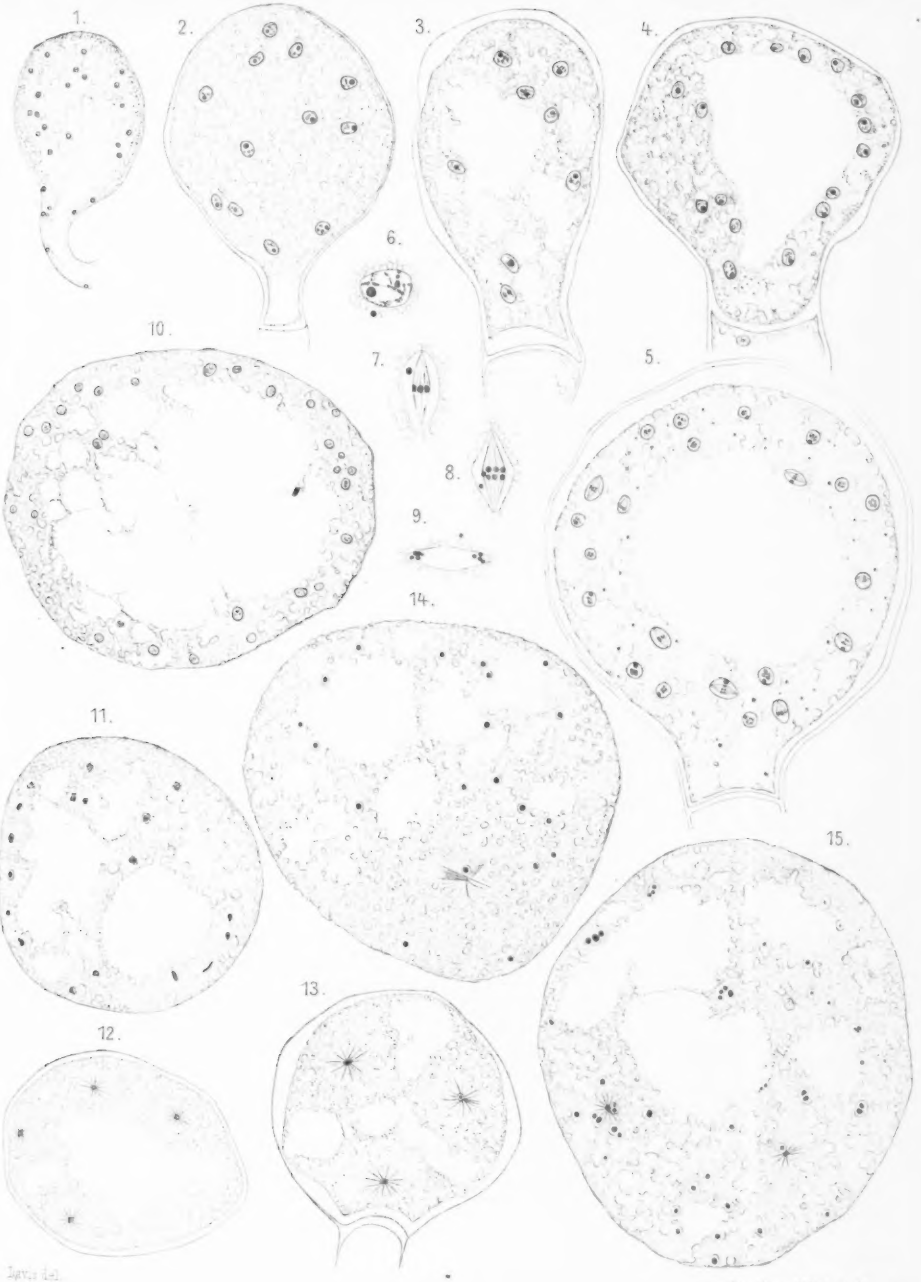
Except for a recent paper by Timberlake (1902) on Hydrodictyon, we know little of the details of zoospore formation in either algae or fungi, and the field would certainly repay investigation. The writer examined the sporangium of *Saprolegnia mixta* to contrast the conditions there with the processes of oogenesis, but, the subject not being favorable, little came of the study, except a general confirmation of the accounts of sporogenesis given by Rothert (1888), Hartog (1888), and Humphrey (1892). If the oogonium is the homologue of the sporan-

gium, we should expect a general similarity in the protoplasmic activities of each structure. There is the general agreement that the protoplasm segments by cleavage planes determined chiefly by vacuoles; but beyond this the activities of the two structures have little in common and a great many peculiarities.

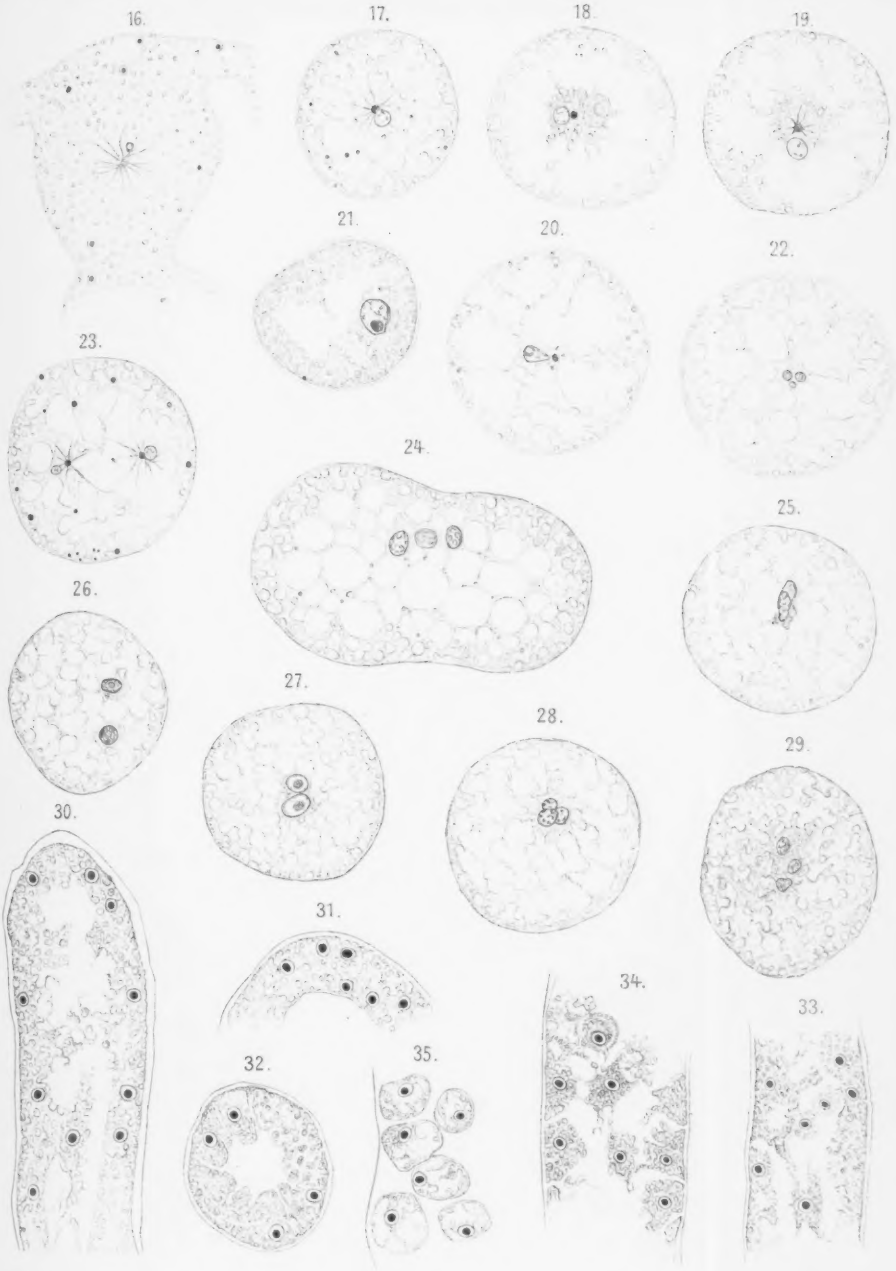
As is well known, there is no mitosis in the sporangium. A large number of nuclei are carried into the tip of the hypha by the accumulation of protoplasm there. Vacuoles collect and develop in the center of the young sporangium (*fig. 30*), and flowing together form a large central space inclosed in a vacuolar membrane (*fig. 31*). The nuclei then lie scattered in the peripheral layer of protoplasm, and presently clefts appear which work outward between the nuclei from the central vacuole (*fig. 32*). The clefts divide the protoplasm so that it is cut up into polygonal areas, with clearer regions between. These are the zoospore origins, and each contains a nucleus.

Rothert's explanations of succeeding conditions, which have also been confirmed by Humphrey and Hartog, seem entirely satisfactory. The sporangium is in a state of turgor when the clefts arise and push their way from the central vacuole toward the periphery. They finally reach the cell wall and immediately make possible the relief of the fluid in the central vacuole. There is at once a very evident decrease in turgor, which has an interesting effect on the appearance of the spore origins. The polygonal areas run together, and the whole sporangium becomes again almost homogeneous in structure. This means that the contraction of the sporangium brings the spore origins so close together that the clefts become almost obliterated. The spore origins also swell. They then begin to separate slowly, preliminary to their being finally rounded off as zoospores. There is a period when the small masses of protoplasm form a very irregular network through the sporangium (*fig. 33*), and this is followed by a more regular arrangement (*fig. 34*), in which the spore origins are connected by very delicate protoplasmic strands. The latter are finally broken and the bodies round off as zoospores.

The writer searched persistently in the sporangium for cyto-



DAVIS on SAPROLEGNIA



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DAVIS on SAPROLEGNIA

plasmic centers around which the process of segmentation might proceed, in the hope that light would be thrown upon the problem of the coenocentrum, but the examination brought forth no evidence of such structures in the sporangium. The nuclei themselves seem to be the ultimate centers of segmentation. The coenocentrum, therefore, so far as we know, is a structure peculiar to the oogonium.

[*To be concluded.*]

THE BEHAVIOR OF THE CHROMOSOMES IN THE SPORE MOTHER-CELLS OF HIGHER PLANTS AND THE HOMOLOGY OF THE POLLEN AND EMBRYO-SAC MOTHER-CELLS.

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(WITH PLATES XI–XIV.)

THERE is probably no other problem which has presented greater difficulties to the botanical cytologist than the behavior of the chromosomes during the two successive nuclear divisions in the spore mother-cells of the higher plants. This is at once apparent, even to those who are not specialists in this field, from the different interpretations which have been advanced from time to time, and from the various and contradictory doctrines that are still held by different investigators.

From the zoological side, we are indebted to Flemming and his students for the first correct interpretation of the behavior of the chromosomes in the two successive nuclear divisions in the spermatocyte of Salamandra.

Flemming designated the first of these divisions as "heterotypic" and the second as "homotypic." The first division in Salamandra is characterized by a long period of growth of the cell and nucleus during the prophase, the appearance of the reduced number of chromosomes and their double longitudinal splitting; the first longitudinal fission taking place during the prophase and the second during the metaphase or anaphase.

The striking parallel between the first two mitoses in the micro- and macrospore mother-cells of higher plants and those of the spermatocyte of Salamandra has frequently been pointed out, and the terms heterotypic and homotypic have been appropriately applied to them.

Recent investigations have shown that in the spore mother-cells of certain higher plants the first mitosis is especially characterized also by a long period of growth during the pro-

phase, the first appearance of the reduced number of the chromosomes, and the double longitudinal splitting of the latter.

It is chiefly upon the behavior of the chromosomes during these divisions that the great diversity of opinion rests, and this is not surprising when one realizes the complexity of the problem and the difficulties attending its investigation. However, in certain plants the double character of the daughter segments during the anaphase of the first nuclear division in the pollen mother-cell is so evident that one is surprised that it has been overlooked for so long a time and by so many observers. In all probability, this phenomenon may have been observed by earlier investigators, but as its significance was not understood the double nature of the daughter chromosomes may have been considered more apparent than real.

Heuser ('84) seems to have been the first to call attention to the double character of the daughter chromosomes in the diaster stage of *Tradescantia virginica*, but he interpreted the separation of the daughter segments during metakinesis of the first mitosis as a transverse division.

In 1895 Strasburger, basing his conclusions largely upon a study of Larix, properly explained the V-shaped daughter chromosomes, which so frequently appear during the anaphase of the first division in the spore mother-cell, as the result of a second longitudinal splitting taking place at right angles to the first. Each V-shaped element, therefore, represents two granddaughter chromosomes which remain attached at the ends to which the spindle fibers are fastened, while the opposite ends diverge, forming the V.

Two years later, Strasburger together with the writer abandoned the doctrine of the double longitudinal splitting, and the V- and U-shaped elements were explained as the result of a folding together of the chromosomes, or as a bending during metakinesis or previously, a view which had been held by other observers. Our conclusions were based largely upon the ring- or loop-shaped chromosomes which often occur in other plants, such as Podophyllum and Tradescantia, and upon phenomena observed in the second mitosis of the embryo-sac of *Lilium*

Martagon. In one respect we were correct, for in many cases the V- or U-shaped chromosomes are produced by a bending, either before or during the anaphase, but the fact that the V's and U's are double was overlooked.

Guignard ('99) found that in *Naias major* a second longitudinal fission occurs during metakinesis of the first nuclear division of the pollen mother-cell, and that each retreating daughter chromosome is composed of two rod-shaped granddaughter segments.

Grégoire ('99), in the same year, observed the same to be true for Lilium and Fritillaria.

Strasburger (1900), upon reinvestigating the subject in several different genera and species, found also that his explanation of 1895 was the correct one; for in all plants examined there occur during the first mitosis in the pollen mother-cell two longitudinal divisions of the chromatin, the first occurring, as the writer had very clearly shown, during the early prophase, the second during metakinesis, or while the daughter chromosomes are on their way to the poles. The second longitudinal splitting is a preparation for the second mitosis, which in Lilium does not pass completely into the structure known as the resting stage.

Since the appearance of the publications above cited, I have taken up the problem again, and have followed carefully both mitoses in the pollen mother-cells of *Lilium Martagon*, *L. candidum*, *Podophyllum peltatum*, and *Tradescantia virginica*, together with the corresponding nuclear divisions in the embryo-sac mother-cell of *Lilium Martagon*.

As regards the pollen mother-cell, I am able to confirm the results of Strasburger and the two French observers, namely, that during the first mitosis two longitudinal divisions of the chromosomes take place. I hope, however, to present more clearly certain details of the second mitosis in the pollen mother-cell, together with certain facts which have hitherto been too lightly touched upon, and add also the evidence which the embryo-sac contributes to the problem.

The earlier prophase of karyokinesis has been described in

minute detail, and I have nothing to add to my former account of the process (Mottier, '97). As soon as the chromatin spirem, which has split longitudinally, has segmented into the chromosomes, each chromosome consists in Lilium of two rather long daughter segments. These segments may be variously oriented toward each other even in the same nucleus. Sometimes they may be separated entirely from each other, being connected only by delicate threads; but, as is generally the case, they are more or less closely applied and twisted upon each other (*fig. 1, a*). Again, they may be attached to each other near the middle or at one or both ends. In the latter case, the free ends may diverge variously (*fig. 1, b, c*). It frequently occurs that the opposite ends adhere, while the middle portion bends outward to form loops or rings (*fig. 2, b*). In the majority of instances, it is clear that the daughter chromosomes are twisted upon each other, and to this fact is due many of the peculiar forms to be observed in the spindle stage.

Between the time of the segmentation of the chromatin spirem and the mature spindle, the chromosomes contract somewhat, becoming thereby shorter and thicker. They may lie distributed along the nuclear membrane or irregularly scattered in the nuclear cavity. At this stage, however, we frequently find the daughter segments so oriented toward each other as to present the various other forms often observed in the nuclear plate, such as loops, rings, X's, Y's, etc. With the development of the spindle, which occurs in precisely the manner described in my earlier paper (Mottier, '97), the chromosomes are gradually oriented in the nuclear plate (*fig. 3*). So far as can be determined with absolute certainty, each chromosome, up to the stage of the mature spindle, is composed only of two daughter segments, although in some cases a trace of the second longitudinal fission may be seen in the segments. It was this phenomenon that strengthened my former view that the chromosomes folded upon themselves during the development of the spindle.

As has been shown by numerous observers, the chromosomes arranged in the nuclear plate present various forms and various

modes of attachment to the spindle fibers. In Lilium the most frequently occurring form of chromosome at this stage is that of the two segments rather closely applied and twisted upon each other. They are attached to the spindle at the end, and stand radially to its long axis (*fig.* 2, *a*). The segments are frequently straight and not twisted upon each other.

Numerous instances are met with in which the daughter segments remain adhering at both ends, but separate near the middle, so that a ring or loop results (*fig.* 2, *b*). The segments may separate at one end, when an open ring or loop is formed. Cases are not infrequently observed in which the segments of the ring-shaped chromosomes bend near the middle so that the free ends are brought nearer together, and we have a ring or loop partly folded upon itself. This is true in a measure in *fig.* 2, *b*. The ring- or loop-shaped chromosome is attached to the spindle near one end of the daughter segments, or at a point midway between the ends, rarely at the ends; although such a mode of fastening was occasionally observed. As a rule, however, the rings or loops are placed tangentially upon the spindle.

When the daughter segments diverge at one end but remain closely applied for the remainder of their length, a Y-shaped chromosome results (*fig.* 2, *h*), which is fastened to the spindle as indicated in the figure. An X-shaped chromosome is formed when the segments lie variously crossed with one or both ends diverging (*fig.* 2, *f*). X-shaped chromosomes are not rare in which the segments are so closely applied at one end as to give the impression of a loop formed by the chromosome folding in such a way that the opposite ends are brought together (*fig.* 2, *g*). In fact all intermediate forms are found between that of *f* and *g*. Finally chromosomes such as *fig.* 2, *c*, *d*, *e* are of frequent occurrence. In this form of chromosome, the segments, which are more or less twisted upon themselves, are usually fastened to the spindle fibers near one end or at the middle. Such chromosomes are, as a rule, oriented tangentially upon the spindle.

As regards the development of the spindle, I have nothing

to add to my account of this process already published (Mottier, '97, '98). There are no individualized centrospheres or centrosomes. It may be mentioned further that in the mature spindle the following arrangement of fibers is to be observed: bundles of fibers extend from the chromosomes to the poles, a complex of fibers running uninterruptedly from pole to pole, the central spindle fibers, and those which diverge from the poles toward the plasma-membrane (*figs. 4, 5, 7*).

During metakinesis the daughter segments undergo a longitudinal fission which is at right angles to the plane of the first longitudinal splitting. In favorable cases, the result of this second longitudinal fission may be seen just as the daughter segments begin to separate or a little earlier, but as a rule the double nature of the daughter chromosomes is not evident until they have separated somewhat (*fig. 5*). As the daughter chromosomes separate, the granddaughter segments remain attached at the polar ends while the opposite ends generally diverge, and the well-known V-shaped structure is the result. In *fig. 5* it is clear that the V-shaped daughter chromosomes owe this form to the manner in which they are attached to the spindle and to the longitudinal fission of each daughter segment into granddaughter chromosomes. The chromosomes at this stage are confusing, because of the distortion of the segments due to the former twisting, and because of the fact that different forms of chromosomes with their various modes of attachment to the spindle occur in the same karyokinetic figure. It should never be forgotten, however, that under the circumstances just described in *fig. 5* the daughter chromosomes as they pass toward the poles are not always V's, but frequently straight or nearly straight rods which lie parallel and closely applied to each other (*fig. 8*, the chromosome in the middle). If the chromosomes be fastened to the spindle by the ends, the daughter chromosomes will form V's only when the equatorial ends of the granddaughter segments diverge.

In such chromosomes as *fig. 2, c. d, e*, it is apparent that the retreating daughter chromosomes may be either in the form of a U or V, and that this form will arise as a bending of the seg-

ments during metakinesis, since they are not attached by the ends. But such U's or V's are always double, as is shown in *fig. 6* on the left, and in *fig. 8*. Both limbs of the U or V are not necessarily of the same length, for there is every gradation between these forms and straight rods with slightly hooked ends.

The double character of the U-shaped daughter chromosome is not always very evident. Sometimes the granddaughter segments give the impression that one chromosome is lying just beneath another. Such phenomena were frequently observed by myself during my first investigation of the subject and were interpreted as two different daughter chromosomes, one lying directly below the other. Chromosomes which have the form of *fig. 2, c, d, e*, will probably yield U- or V-shaped elements as a result of being bent during metakinesis. The X and Y forms (*fig. 2, g, h*) will probably give rise also to V-, rod-, or hook-shaped elements. In *fig. 6*, the chromosome on the left was attached to the spindle near the middle, and each daughter segment consists of two similar U- or hook-shaped granddaughter elements. This chromosome may have been originally in the form of *fig. 2, b, c*, or the two daughter segments may have sustained the same relation to each other as in the figure, being in contact only at one end. In the chromosome at the right (*fig. 6*), the attachment was at the end, so that each daughter chromosome consists of two similar rods more or less bent or undulating.

Fig. 7 shows a typical nuclear figure in the anaphase. Here it is clear that the chromosomes were attached to the spindle by the ends, or very near the ends, so that as a consequence of the second longitudinal fission each daughter chromosome consists of two rod-like, straight, or variously bent or hooked granddaughter elements, which adhere at the polar ends, while the equatorial ends diverge. Sometimes the polar ends are so closely adherent or fused that the daughter chromosomes may appear as continuous V-shaped objects. In such cases it is often impossible to determine in what manner the V-shaped chromosome was produced, and it is this fact that has led to incorrect interpretations. The close adherence or fusion of the grand-

daughter segments at the ends turned toward the poles may be due to the manner in which the segments are attached to the spindle, as both granddaughter segments are fastened to the same bundle of fibers.

As the pairs of granddaughter elements arrive at the poles, they approach each other so closely that generally the identity of the individual elements can not be recognized, but in many cases the reconstruction of the daughter spirem can be followed with precision. I have already shown how the free ends of the daughter chromosomes unite to form a single daughter spirem (*fig. 10*). If the granddaughter segments form V's, the ends at the angle fuse first, in case this has not already happened, and then follows the fusion of the free ends. But in those cases in which the granddaughter segments are U-shaped and closely applied to each other side by side, it is evident that they must first separate in order to unite end to end, for the spirem was always found to be single.

At first the spirem is contracted, consisting of short turns, but soon after the nuclear membrane is laid down, the spirem becomes hollow and more regular and uniform.

Grégoire ('99) states with emphasis that in *Lilium candidum* and *L. speciosum* especially the chromosomes maintain their identity throughout in the daughter nucleus; that a continuous spirem is not formed but only a pseudo-spirem. My studies have included *L. candidum* and *Fritillaria persica*, and in these, as well as in *L. Martagon*, nothing is clearer than the fact that the chromosomes do lose their identity in the daughter nucleus.

The chromatin thread is not at all times an even and uniform spirem. During the reconstruction of the daughter nucleus, the chromosomes show a tendency to reticulate, becoming somewhat lumpy, and the spirem, if we may so designate the chromatin at this stage, is interrupted in many places. This is true especially just after the spirem begins to become more hollow, and the phenomenon may be regarded as a tendency to pass into the structure of the resting nucleus. The tendency of the nucleus to go into the resting stage is more pronounced in the embryo-sac and in other plants to be mentioned in a later paragraph.

In some cases and at a later stage a large part of the daughter spirem is quite regular, presenting a series of long and more or less uniform turns, so that when seen from the pole, the spirem appears in the form of a wreath or crown (*fig. 11*). This regularity is rather the exception than the rule, since in the majority of cases much of the spirem consists of irregular turns varying in size. It seems probable that were all the granddaughter elements rods, which form V's, the spirem would be quite regular; but, as often happens, when these elements arrive at the poles in the form of V's, double U's, and contorted rods intermingled, a very irregular spirem must result.

Strasburger, Guignard, and Grégoire state without reserve that the loops of the spirem (*fig. 11*) represent the V's and U's of the previous karyokinesis. This may be true, but the statement for Lilium, and more especially for other plants to be mentioned later, is purely a deduction. The spirem is often, if not always, continuous, as Strasburger also asserts, and the identity of the individual chromosomes is lost. It is true that in Lilium the daughter nucleus does not pass into that structure known as the complete resting stage, yet during the construction of the daughter spirem the chromosomes do to some extent become reticulated, so that the second mitosis may have for its purpose something more than the equal distribution of the granddaughter chromosomes to the four granddaughter nuclei. This seems especially true in those plants in which the daughter nuclei pass into the resting stage or approach it more closely than in Lilium.

The division of the daughter nucleus in the pollen mother-cell of Lilium and in other phanerogams as well, has been a stumbling block to every cytologist who has studied the problem. So complex is the process, especially the behavior of the chromatin, and so numerous are the difficulties attendant upon its study, that it is little wonder that errors have been made and that several different explanations have seemed at the time equally correct.

As I have shown in former publications, the spindle of the second mitosis develops as a multipolar structure, arising in a

manner similar to that of the first division. Attention was called to the fact also that the spindle fibers may enter the nuclear cavity before the spirem is completely segmented into the chromosomes, this being the case in both the pollen and embryo-sac mother-cells, and my present studies have only confirmed this statement.

Grégoire claims that in *Lilium candidum* and *L. speciosum* the chromosomes become isolated and independent before the nuclear membrane has disappeared. In some cases in *Lilium candidum* and *Fritillaria persica* it seems that the chromosomes are isolated before the nuclear membrane disappears, but this is rarely the case in *L. Martagon*. Moreover, no special importance has been attributed to the fact that the spindle fibers enter the nucleus in some cases before the individual chromosomes are completely isolated. It is not necessary, however, to demonstrate the identity of the chromosomes throughout the second mitosis to show conclusively that two longitudinal divisions of the chromatin occur during the first mitosis.

After the nuclear membrane has disappeared and the multipolar spindle complex is laid down, or in the process of formation, the chromosomes are, as a rule, so closely entangled, kinked, and twisted that it is impossible to trace them save in exceptional cases. For this reason it is extremely difficult, if not impossible, to determine beyond all doubt the manner in which they are formed from the spirem. *Fig. 12* represents a section of a daughter nucleus in the multipolar stage of the spindle. In this case the spirem is more loosely arranged, and many of the loops and turns may be traced with greater accuracy than in the vast majority of instances. From this and *figs. 13*, *14*, and *15*, it is evident that the two segments of each chromosome in the nuclear plate represent probably the two parallel limbs of the loops observed at an earlier stage, which have become more or less closely applied to and sometimes twisted upon each other. The fact that the turns of the spirem in the daughter nucleus are not all regular and uniform accounts for the twisted and entangled condition of the chromosomes during the formation of the spindle. In the mature spindle (*figs. 14*, *15*) the chromo-

somes are arranged both radially and tangentially. The two elements of each chromosome may lie parallel with each other, or they may remain almost entirely separate, being in contact only at the ends that are attached to the spindle fibers (*fig. 14*). This seems to be more frequently the case in *Lilium candidum* and Fritillaria. In the latter arrangement both elements may lie upon the same side or upon opposite sides of the equatorial plane. The chromosomes are fastened to the spindle fibers at or near the ends, rarely near the middle. When they are fastened near the ends, these are generally bent somewhat so that the retreating segments appear in the form of rods which are slightly hooked at the ends turned toward the poles (*fig. 17*).

Strasburger (1900), Guignard, ('99), and Grégoire ('99) claim that the two segments of each chromosome in the second division correspond exactly to the pairs of granddaughter segments which form the V's or U's of the first mitosis, and that they are fastened to the spindle at the places of bending or at the angles of the V's as in the first mitosis. Theoretically there may be little objection to this statement, as the matter in question may be a detail of secondary importance, but it seems that the observed facts will not admit of its general application in Lilium. *Figs. 13, 14,* and *15* show clearly that the free ends of the loops or V's are as likely to be attached to the spindle. Furthermore, we cannot say with certainty that the chromosomes of the second mitosis are identical with the pairs of granddaughter elements of the first division, for it does not seem impossible that the spirem may segment in such a manner that the segments of each chromosome of the second division may be derived from different pairs of granddaughter elements.

This may be brought about by the spirem segmenting at the apex of the V's rather than at the points corresponding to the free ends of the elements of each V, assuming that each long loop of the spirem represents a V. Under such circumstances, if all the granddaughter elements composing the spirem were so oriented in the preceding anaphase as to form V's, then all of the chromosomes of the second division would be made up of elements from different pairs of sister segments. But on the

other hand, should the spirem segment in some places at the points corresponding to the angles of the V's, and at others which represent the points of contact of the free ends of the V-shaped chromosome, then some of the chromosomes of the second division would be composed of sister segments while others would not. If either of the last named possibilities be true, it might very easily happen that sister segments would go to the same granddaughter nucleus, a condition that might furnish a probable basis for a greater variation. Even though the latter supposition be true — that some or all of the chromosomes are not sister segments — it is possible that the results would be the same, for the spindle, or whatever part of the cell that has to do with the distribution of the chromosomes, may be able to prevent any such mixing by distributing to the granddaughter nuclei those chromatin elements which would unavoidably go to each if every chromosome were identical with the pairs of sister segments of the preceding division.

But since the chromosomes lose their identity in the daughter nucleus, neither of the foregoing suppositions can be objectively demonstrated. This is not possible, as yet, even in those cases in which the spirem is very regular or in plants with fewer chromosomes, and the possibility is still farther removed in those cases of more frequent occurrence in which the spirem is very irregular.

In the foregoing statements the writer does not intend to convey the idea that he rejects the older view, but the doctrine is advanced largely as a probability which seems to have some basis in fact. The older view, that the chromosomes of the nuclear plate of the second mitosis are identical with the pairs of granddaughter segments of the first division, is the simpler hypothesis, involving fewer complications, and for that reason it may be more readily accepted. Its truth, however, can be no more definitely demonstrated than that which I have suggested as a possibility, for there is no known angiosperm, so far as the writer is aware, in which the chromosomes of the first division do not lose their identity in the daughter nucleus, and we do not know with absolute certainty whether the daughter spirem seg-

ments in such a manner that the resulting pairs of segments are identical with the pairs of granddaughter segments of the first division. In those cases to be mentioned in a later paragraph, in which the daughter nucleus closely approaches or passes into the resting stage, it is readily seen how much more difficult the problem is.

A glance at those stages of the process represented in *figs. 12, 13, 14,* and *15* will give some idea of how the long and entangled chromatin segments are gradually brought to a more regular arrangement in the nuclear plate, although in species of Lilium with long chromosomes the arrangement, as a rule, is not very regular. The twisted and contorted form of the chromosomes seems to be due chiefly to the irregularity of the spirem.

During the transformation of the multipolar into the bipolar spindle, the entangled collection of chromosomes seems to be gradually pulled, pushed, and untangled into the more regular arrangement of the equatorial region, and there can be little doubt that the spindle fibers are primarily active in bringing each pair of chromosomes into its proper place.

As already stated, the segments of the chromosomes in the nuclear plate lie generally side by side and more or less twisted about each other. Sometimes the free ends of the segments diverge widely, those which are fastened to the spindle fibers being in contact or even separated a little. This phenomenon has been interpreted by some observers as metakinesis, but such a condition is sometimes met with before the spindle is mature. The spindle fibers have an orientation similar to that of the first mitosis.

As the segments separate during metakinesis, the nuclear plate presents a complicated picture (*fig. 16*). This phenomenon is due to the twisted condition of the chromosomes previously mentioned. On their way to the poles the segments may straighten out somewhat. Each is then usually a long and frequently undulating or bent rod, that is generally hooked at the end to which the spindle fibers are attached (*figs. 17, 18*). Sometimes the chromosomes are attached near the middle, in which case the retreating segments will be in the form of a V or a U.

The formation of the granddaughter nuclei presents nothing which demands a special mention.

Confining himself to the study of the chromosomes in Lilium alone, the investigator would undoubtedly hesitate long before concluding in favor of the double longitudinal splitting of the chromosomes during the first mitosis, because of the variety existing in the form of the chromosomes and their orientation upon the spindle, the difficulty with which the double nature of the V-shaped elements which owe their form to a bending is generally recognized, and because of the extremely complicated character of the chromatin spirem during certain important stages of the second mitosis. The phenomena presented in *Podophyllum peltatum* and *Tradescantia virginica* leave no doubt whatever as to the correctness of this view.

The development of the chromosomes during the prophase of the first division in Podophyllum, as well as other important detail of karyokinesis, have already been fully described in my earlier paper (Mottier, '97), so that only enough of the process will be given here to bring out clearly the behavior of the chromosomes.

Soon after the segmentation of the spirem into chromosomes the daughter segments tend to become separated except at one or both ends, or they may adhere only near the middle and both ends diverge, as the daughter segments are usually somewhat curved. They may also remain in contact for their entire length, but this is less frequently the case. When the chromosomes are arranged in the nuclear plate they lie, as a rule, tangentially upon the spindle. The daughter segments are more frequently observed adhering at one end only, as in *fig. 20*, but, as in Lilium, should the segments adhere at both ends, the ring-shaped chromosome is the result (*fig. 19*). It not infrequently happens that both forms of chromosomes are seen in the same nuclear figure. *Figs. 19* and *20* show the manner in which these chromosomes are fastened to the spindle fibers. In those cases in which the daughter segments adhere only at one end, the ends in contact are so closely applied as to give the appearance of a lump or swollen place. This is especially true when the ends of the curved segments are turned directly toward or away from the

observer. In case the daughter segments are in contact for their entire length the chromosomes may be fastened to the spindle at one end and arranged radially upon it; but, as a rule, the point of attachment is at the place of bending, whether that be near one end or at the middle of each segment. The X-, Y-, and U-shaped chromosomes, although of less frequent occurrence in Podophyllum, are formed in the same manner as described for Lilium.

During the metaphase, or immediately following it, each daughter chromosome is seen to be double or composed of two similar granddaughter segments, the result of the second longitudinal splitting (*figs. 22, 23*). The shape of the pairs of granddaughter segments will, of course, depend upon that of the daughter chromosome. In *fig. 21, a*, it is evident that this chromosome before metakinesis was similar to those in *fig. 20*. In *fig. 21, b*, the daughter segments may have been in contact throughout and the chromosomes fastened to the spindle at the end. The retreating pairs of segments in this case may present the familiar V's. The chromosome to the right in *fig. 22* was either in the form of a ring or a U when in the nuclear plate. This condition was observed at the time of my earlier study upon Podophyllum, but such conditions were interpreted as two similar but different chromosomes lying close together, one beneath the other.

The double nature of the daughter chromosomes can be clearly distinguished until they reach the poles. Having arrived at the poles, they generally become closely crowded together so that the individuals are difficult to distinguish. It can be seen, however, that the segments of each pair tend to separate, and there was nothing observed which might lead one to conclude with any certainty that a double spirem is formed. The granddaughter segments in forming the spirem tend to reticulate somewhat so that they become irregular in shape and their exact identity is lost. Those observers who assert without reserve that the identity of the chromosomes can be followed at all times from one division to the other, certainly leave this fact and other steps of the process out of consideration.

In a short time, a more regular spirem is formed in which parallel or adjacent portions are frequently connected by fine threads. As I have already shown, the spindle of the second division arises as a multipolar structure (*fig. 26*). During the formation of the spindle, the chromatin spirem segments into the chromosomes. The segments are collected together within the complex of spindle fibers so that the manner of segmentation can not be determined with certainty. The same would be true if the spirem segments before the nuclear membrane had disappeared, and it is a matter of little importance whether the spirem segments before or after the disappearance of the nuclear membrane. In many cases it seems that the spirem breaks up into pieces equal in length to the two segments of the chromosomes, but this does not always appear to be true (*fig. 26*). However, during the transformation of the multipolar complex of fibers into the bipolar spindle, the chromosomes are gradually arranged more regularly into the nuclear plate (*figs. 27, 28*). Each chromosome consists now of two similar segments which may or may not be closely applied to each other. Instances have been observed in which the two segments of a chromosome were of a slightly different length. The chromosomes are probably identical with the pairs of granddaughter segments of the first division, but here, as in Lilium, we do not know definitely whether the two segments of each chromosome are sisters. The chromosomes are mostly in the form of rather thick rods more or less curved. They are fastened to the spindle fibers near the ends or at the place of bending. The retreating segments, therefore, may be nearly straight, hooked, V- or U-shaped.

Among monocotyledonous plants, apart from the lilies, few perhaps are more suitable to demonstrate the fact of a double longitudinal splitting of the chromosomes during the first mitosis in the pollen mother-cells than *Tradescantia virginica*.

Between the time of the segmentation of the chromatin thread into chromosomes and the development of the spindle, the chromosomes contract greatly, becoming shorter and thicker. The daughter segments tend to separate except at one or both ends. In case they adhere at both ends, a ring or ring-like chromo-

some results. At the time of or even before the formation of the spindle, the daughter segments contract to such an extent that each may be in the form of a short, thick crescent. Each ring-like chromosome will therefore consist of two crescents whose ends adhere (*fig. 30*). It not infrequently happens that the daughter segments contract in such a manner that closed rings are formed. If the daughter segments remain adhering at one end, each chromosome in the nuclear plate is seen to consist of two thick pieces in the form of either a short crescent, a broad U, or only slightly bent at one or both ends (*fig. 31*, on the left). Under these circumstances the whole chromosome is relatively long, reaching almost from pole to pole.

As a rule the chromosomes are oriented tangentially upon the spindle, the fibers being fastened at the middle of each segment or near one end. It is interesting to note that the place to which the fibers are attached is almost always in the form of a small protuberance, giving the impression that a pull is exerted by the spindle fibers. In *fig. 30* is shown the singular phenomenon of two chromosomes fastened together, a fact which is of course without any special significance.

No indication of a second longitudinal splitting is seen in Tradescantia when the chromosomes are in the nuclear plate, and, so far as could be determined with certainty, not even during metakinesis, although it may occur here as early as in Lilium (*figs. 30, 32*); but by the time the daughter chromosomes have traversed one-half the distance toward the poles, it can be usually seen that each consists of a pair of granddaughter segments, arising from the second longitudinal splitting (*fig. 33*).

Having arrived at the poles, the pairs of granddaughter segments become somewhat crowded together, and shortly the nuclear membrane is laid down (*fig. 35*). The segments, or some of them at least, now separate slightly; but as they begin to reticulate, becoming lumpy and very irregular, their identity is soon lost. The process of reticulation continues, and at a little later stage the lumpy chromatin masses which are connected by numerous fine threads present the appearance of *fig. 36*. As in many other plants, there is not an even and uniform

spirem formed at once from the segments of the daughter chromosomes. The reticulation continues, at least in many cases observed, until a structure is reached that is certainly very near that of a resting nucleus. *Fig. 37* represents a nucleus seen from the pole. If the same nucleus were observed from the side, at this or even a little earlier stage, its chromatin would present the appearance of a rather thick and irregular spirem.

There are phenomena in Tradescantia which would suggest that the daughter spirem or parts of it are formed double, but all the evidence taken together seems to indicate that only a single spirem is the result. Daughter nuclei were observed in which certain parts of the spirem, or chromatin thread, seemed to be double, while other parts showed nothing of a double character. The chromatin of the daughter nucleus does not form the regular and uniform spirem to be observed in other monocotyledonous species and in Podophyllum, and for this reason the differentiation of the chromosomes is followed with greater uncertainty. With the approach of the second mitosis, the chromosomes are differentiated and lie distributed in the nuclear cavity before the disappearance of the nuclear membrane. They are often very irregular in shape and connected by delicate linin threads. Even when arranged in the nuclear plate, they present an irregular, lumpy, and twisted form. In those cases in which the chromosomes are most regular, each is seen to consist of a pair of rod-shaped segments which are either straight with only a slight bend at one end, or more or less undulating and twisted (*fig. 39*). As in Lilium, some of the chromosomes are oriented radially and some tangentially upon the spindle.

It may be that the two segments composing each chromosome are sisters, and that the chromosomes are identical with the pairs of granddaughter segments of the first division, but the possibility of an objective demonstration of this supposition seems out of the question.

The process of the second karyokinesis in the pollen mother-cells of other plants seems to suggest strongly that the division of the daughter nuclei has some other purpose than merely the

distribution of an equal number of chromosomes to the four granddaughter nuclei.

In 1898, the writer showed clearly the striking similarity between the first two mitoses in the micro- and macrospore mother-cells of *Helleborus foetidus* and *Lilium Martagon*, and concluded upon that evidence that the pollen and embryo-sac mother-cells were homologous. The work of recent observers, especially Juel (1900) and Schniewind-Thies (1901), who have confined their attention primarily to this phase of the problem, has only confirmed this view.

Since the chromosomes in the pollen mother-cell undergo a double longitudinal division during the first or heterotypic mitosis, the same would seem certain also in the embryo-sac mother-cell, and it was for this reason that a reinvestigation of the problem in *Lilium Martagon* was undertaken.

As was expected, the first and second mitoses in the embryo-sac were found to be essentially like those in the pollen mother-cell. These divisions will be described somewhat in detail in order to show what the embryo-sac contributes toward the solution of this and other problems suggested in the preceding pages.

As is well known, the mother-cell of the embryo-sac of Lilium becomes the macrospore and develops at once into the embryo-sac. The first nuclear division is heterotypic, the nucleus undergoing the same changes during the prophase as in the pollen mother-cell. The spindle arises as a multipolar structure, and the form and orientation of the chromosomes within the multipolar complex of fibers and upon the mature spindle present nothing requiring a special description.

Owing to the small number of macrospores in an ovary as compared with the number of microspore mother-cells in an anther, a much smaller number of karyokinetic figures will be observed in the former, yet in the course of an extended investigation, it seems exceedingly probable that about the same variety in the form of the chromosomes exists in the macro- as in the microspore mother-cell. As a rule, the daughter segments are twisted upon each other and fastened to the spindle fibers by the ends (*fig. 40*). Only in exceptional cases can any indication of

the second longitudinal splitting be discerned before metakinesis. As soon as the daughter chromosomes separate, however, each is seen to consist of two similar granddaughter segments. The figures which these pairs of segments present will depend, of course, upon the orientation of the daughter chromosomes toward each other, their shape, and mode of attachment to the spindle fibers.

The retreating segments, therefore, may form V's, U's, or more or less contiguous rods, which may be undulating or abruptly bent, and, as is sometimes the case, hooked at the ends directed towards the poles (*fig. 41*).

Having reached the poles, the granddaughter segments do not, at least as far as my observations have extended, form immediately a regular spirem of a uniform thickness, but there is here a greater tendency on the part of the chromatin elements to become reticulated and pass into a structure closely approaching that of a resting nucleus. This was found to be true in all cases observed. As will be seen from *fig. 42*, the two daughter nuclei present a structure which is certainly very near that of a resting nucleus. Several nucleoli are present, and there is no regular, continuous spirem. Although the nuclear thread may be continuous, yet the chromatin is in the form of granules that are of a very variable size and unevenly distributed. Certain portions of the nuclear thread contain apparently a single row of small chromatin granules, as in an early prophase of karyokinesis; in other portions two rows of these granules are present, while still other parts are thicker and somewhat lumpy.

In the light of all the facts observed, nothing seems more certain than that in the daughter nuclei all identity of the chromosomes is lost from observation. While it is true that a greater pause intervenes or seems to exist between succeeding nuclear divisions than between the first and second mitoses, yet it does not follow that the second division takes place immediately after the first without a resting pause.

As regards the details of further karyokinetic activity in the embryo-sac, I am able to add little to my former observations. As already mentioned (Mottier, '98), the second mitosis bears

certain striking resemblances to that in the pollen mother-cell. In all probability they are exactly the same. In the chromatin spirem no indication of a longitudinal splitting is to be seen. The nuclear membrane disappears as such, and the spindle fibers penetrate the nuclear cavity before the spirem is segmented into chromosomes (*fig. 43*). The complete segmentation seems to be effected later than in the pollen mother-cell. Within the multipolar complex of spindle fibers the partly segmented spirem, as in the pollen mother-cell, is generally greatly entangled and kinked. As the spindle matures, the arrangement of the chromosomes becomes more regular, but, as a rule, less so than in *fig. 44*. When the spindle has reached the typical bipolar stage, the chromosomes are oriented in the nuclear plate, some radially and some tangentially (*fig. 44*).

Each consists of two rather long and closely applied segments that may be twisted upon each other. It seems that the spirem may not be entirely segmented even when the typical bipolar stage of the spindle is reached (*fig. 44*), and as the apparently unsegmented portions are double nothing seems more reasonable than the conclusion that the double nature is due to the longitudinal splitting of the chromatin spirem, and it was upon this evidence that my conclusion of 1898 was based, namely, that the spirem of the daughter nucleus undergoes a longitudinal fission.

Since the second longitudinal fission takes place during the first mitosis, it is not difficult to understand, especially when one bears in mind the entangled or kinked condition of much of the spirem during the development of the spindle, and the fact that portions of it are very slender, appearing as if stretched by the fibers, how parallel portions of the spirem may be so brought in contact as to look like a longitudinal splitting had occurred. Further evidence in favor of the doctrine that the two segments of each chromosome are brought in contact side by side, is the fact that in both pollen and embryo-sac mother-cells one very frequently meets with chromosomes that do not consist of two rather straight and readily distinguishable segments, but rather short, thick, and lumpy chromosomes which show that the segments are kinked or twisted up into a short spiral or coil. It

seems furthermore exceedingly probable that the longer and more uniform turns of the spirem will furnish the regular and straight chromosomes, whilst the less regular parts — for such exist in the majority of the daughter nuclei in question — give rise to the short, kinked, or knotted ones.

It may be mentioned in passing that every step in the development of the spindle seems to bear direct evidence in favor of the view that the arrangement of the chromosomes is accomplished by a pushing and pulling action of the spindle fibers.

Relative to the behavior of the chromatin, it may be stated finally that the possibility is not excluded that in some cases the spirem may be formed double, in part or entirely, but direct evidence of such a possibility was not observed save in the presence of two rows of chromatin granules in portions of the thread-work of the daughter nucleus.

The daughter nucleus in the lower end of the embryo-sac, which gives rise ultimately to the antipodal cells and the lower polar nucleus, behaves in division exactly as the upper, and the fact that this nucleus presents a larger number of chromosomes only adds more difficulties to the problem of the chromosomes.

In certain respects, the third karyokinesis in the embryo-sac of *Lilium Martagon* resembles the second. This is true as regards the development of the spindle whose fibers penetrate the nuclear cavity before the chromatin spirem is entirely segmented into the chromosomes (see Mottier, '98, *figs. 16, 17*). The behavior of the chromatin, however, is quite like that in ordinary and typical vegetative cells.

The first two mitoses in the spore mother-cells of higher plants, therefore, are heterotypic and homotypic respectively, these terms being used in the sense of Flemming. The chief distinguishing characteristic of the heterotypic nuclear division is the double longitudinal fission of the chromosomes. The shape of the chromosomes is without importance, since the form of the individual chromatin elements, which often varies in the same nucleus, is due to different causes. This division is further characterized in plants by a rather long period of growth during the prophase which results in a marked increase in the size of

the nucleus and in the quantity of chromatin substance. In the higher plants, it is during this division that the reduced number of chromosomes appears.

In the homotypic division, the chromatin spirem or thread does not undergo a longitudinal fission. During the development of the spindle the granddaughter chromosomes are arranged in pairs in the nuclear plate by means of the spindle fibers. The segments of each pair often lie closely applied side by side in such a way as to suggest that the daughter spirem had split longitudinally. This arrangement of the segments with reference to each other does not always obtain, for they may frequently diverge, one lying tangentially upon one side of the equator and the other upon the other side. In the pollen mother-cell of Lilium and in certain other plants, the homotypic may follow the heterotypic division without the intervention of a complete resting stage, but even here there is a greater or less tendency for the daughter nucleus to pass into the structure of the resting condition. In all cases, however, the identity of the individual chromosomes is lost from observation in the daughter nucleus.

THE HOMOLOGY OF THE MICRO- AND MACROSPORE MOTHER-CELLS.

From the foregoing statements and in the light of the recent researches of Juel (1900) and Schniewind-Thies (1900), it seems that all cytological evidence indicates clearly and unmistakably that the pollen mother-cell and embryo-sac mother-cell are homologous.

The writer has already shown that the first nuclear division in the macrospore mother-cell of Helleborus is heterotypic, and the same is true for Podophyllum. In the development of the embryo-sac of Helleborus, which may be regarded as typical for dicotyledonous plants, as well as for many monocotyledonous species, the heterotypic and homotypic mitoses are each followed by cell-divisions, giving rise to four potential macrospores, homologous with the four granddaughter cells in the pollen mother-cell. The fact that occasionally in Helleborus cell-division does not take place until after the second mitosis

serves to show more definitely the close resemblance between embryo-sac and pollen mother-cell (Mottier, '98, *fig. 31*).

Juel (1900) has shown that the two successive divisions in the macrospore mother-cell of Larix gives rise to four cells in the same manner as in such angiosperms as Helleborus, and that the first of these mitoses is heterotypic. This is probably true for many other gymnosperms.

It is well known that the developmental history of the embryo-sac between the macrospore mother-cell and the mature female gametophyte is shortened in certain cases by one or two nuclear divisions, and it is important to know, in these cases of abbreviated development, the place occupied by the two mitoses in question.

With this object in view Frau Schniewind-Thies (1900) has investigated the development of the embryo-sac in several species of the Liliaceae, and has brought together a number of interesting observations. In all cases examined by this author, the first two nuclear divisions in the mother-cell are heterotypic and homotypic respectively, and whenever four potential spores result, each nuclear division is followed by a cell-division. One of these potential macrospores, usually the lower one, develops, as in Helleborus, by three successive typical or ordinary mitoses into the embryo-sac. In the case of *Scilla sibirica*, however, the developmental history of the female gametophyte, or embryo-sac, is shortened by only one nuclear division. The first or heterotypic division is followed by a cell-division. Following the second, or homotypic mitosis, no cell-division takes place, and consequently each daughter cell contains two nuclei. Either of these cells may function as the macrospore, and develop into the embryo-sac, while the other is absorbed. In this case the homotypic division represents the first mitosis in the spore. The two daughter nuclei now divide twice in the typical way to give rise to the mature embryo-sac. In *Scilla sibirica*, therefore, there is a shortening of the development by one typical mitosis.

In Lilium and in other genera with a similar development of the embryo-sac, the process is further shortened. Here the macrospore mother-cell functions at once as the spore. No cell

division follows the heterotypic or homotypic mitoses, although there is sometimes a tendency toward cell-plate formation (Mottier, '98), and these two nuclear divisions represent two out of the three divisions in the embryo-sac.

In the light of these facts, it seems clear that in Lilium there is merely a shortening of the development of the embryo-sac by two typical mitoses.

The development of the embryo-sac immediately from the mother-cell has probably no parallel in the case of the pollen, since Strasburger (1901) and Frye (1901) have recently shown that in Asclepias and in a few other genera, in which the pollen mother-cell was supposed to function as the spore, the usual process of the development of the pollen obtains.

SUMMARY.

In the karyokinetic processes occuring in the micro- and macrospore mother-cells of the angiosperms, certain phenomena may now be regarded as very well understood and pretty definitely established.

In the first place, the nuclear spindle arises as a multipolar complex of fibers, wholly or almost wholly of cytoplasmic origin, which is gradually transformed into the typical bipolar spindle. No centrospheres or centrosomes are present.

During the first mitosis the reduced number of chromosomes appears. There is no reduction or qualitative division in the sense of Weismann. The first division is characterized further by two longitudinal divisions of the chromatin, the second longitudinal splitting being at right angles to the plane of the first.

The first longitudinal fission occurs in the early prophase; the second is demonstrable in the mature spindle when the chromosomes are arranged in the nuclear plate, or first during the meta- or anaphase. Sometimes evidence of the second splitting appears at an earlier stage, but these are not conclusive.

The second longitudinal fission seems to be a preparation for the second or following mitosis.

The first division is also characterized by the long period of

growth during the prophase, resulting in an increase in the size of the nucleus and in the quantity of chromatin.

The granddaughter chromosomes, having arrived at the poles, unite end to end to form a continous daughter spirem in Lilium and in Podophyllum. In all species examined all identity of the individual chromosomes is lost in the daughter nucleus. In Podophyllum and even in Lilium the granddaughter chromosomes show a marked tendency to reticulate, becoming irregular, while in Tradescantia and in the embryo-sac of Lilium the reticulation of the chromatin is continued to such an extent that the daughter nucleus passes almost into the structure of the resting stage.

The chromatin thread or spirem of the daughter nucleus does not undergo a longitudinal fission. During the development of the spindle and in some cases earlier, the daughter spirem segments into the granddaughter chromosomes, which are gradually arranged in pairs in the nuclear plate by means of the spindle fibers. As the granddaughter chromosomes are conveyed to the poles during the anaphase, they are usually in the form of rods, which may be straight, undulating, hooked at one end, or sometimes U- or V-shaped.

The first mitosis in both the micro- and macrospore mother-cells of the higher plants is, therefore, heterotypic, and the second homotypic. These nuclear divisions are not, properly speaking, reducing or reduction divisions. They are not the agents of the reduction, but rather the result of the numerical reduction of the chromosomes.

In the plants which were the objects of investigation, it is clear that the various forms of chromosomes observed in the heterotypic mitosis are such that might suggest more than one valid interpretation, and it is in a large measure due to this fact that there still prevail different and opposing interpretations in plants as well as in animals. The history of the development of the chromosomes, and a more thorough knowledge of their behavior during every phase of karyokinesis have shown that the shape which they may assume is of secondary importance. The form of each chromosome depends chiefly upon the shape of the

daughter segments and their orientation toward each other and the manner in which the chromosome is fastened to the spindle.

In Lilium the daughter segments are, as a rule, rather long rods closely applied to and twisted upon each other. As shown in the preceding pages, there are many variations from the usual form. They are generally fastened to the spindle fibers at the end, and under such circumstances placed radially upon the spindle.

During metakinesis, the second longitudinal fission manifests itself, and each daughter chromosome consists of two granddaughter segments, which usually adhere and sometimes fuse at the ends to which the spindle fibers are fastened, while the opposite ends may diverge to form the V- or U-shaped figures. It often happens that the free ends of the granddaughter segments do not diverge, in which case the retreating daughter chromosome is in the form of two contiguous or nearly contiguous rods. Sometimes the ends of the granddaughter segments appear so completely fused near the place of fastening to the spindle that the daughter chromosome resembles a continuous rod bent into the shape of a V or U. On the other hand, V- and U-shaped daughter chromosomes are brought about by another process, namely, that of a bending. Under this circumstance the chromosomes are attached to the spindle, not by the ends, but near the middle or at some distance from one end, and the orientation upon the spindle is generally tangential. The V- or U-form is then due either to a previous bending of each daughter segment in such a manner as to form a ring or loop, or the bending may be caused by a pushing or pulling of the spindle fibers during the meta- or anaphase. In all such cases the V's or U's so formed are double as a result of the second longitudinal splitting.

The fact that in many plants the daughter nucleus passes into the resting stage would seem to indicate that the second or homotypic mitosis signifies something more than the mere distribution of the granddaughter chromosomes to the granddaughter nuclei. In such cases it is difficult to understand the purpose of two longitudinal fissions during the first karyokinesis.

It is generally assumed that the two granddaughter segments of each chromosome appearing in the nuclear plate of the second mitosis are sisters and identical with the pairs of segments of the anaphase of the first division. This can only be true when the spirem segments in exactly the same manner in which it was constructed, assuming that the pieces separated by the breaking up of the spirem consist of the two segments of each chromosome. But on the other hand, if the spirem break up so that the individual segments are separated from the start, then sister segments may be brought together in pairs in the nuclear plate. It is evident in many instances that the pieces into which the spirem falls does consist of the two segments of each chromosome in the second division, and that these are brought side by side by the folding of the piece or by the two parallel members of a loop or turn approaching each other.

However, as has been pointed out in a preceding paragraph, should the spirem segment in a different manner with each piece representing two segments, the two segments of the chromosomes would not necessarily be sisters. In such cases, the possibility is not excluded that two or more sister chromosomes may fall to the same nucleus. Moreover, as the identity of the individual chromosomes is lost in the daughter nucleus, it is not possible to demonstrate objectively whether the segments are sisters or not.

There is also no basis in fact which will justify the doctrine that one chromosome is qualitatively different from another.

The development of the spindle seems to show that the chromosomes are oriented in the nuclear plate by a pushing and pulling action of the spindle fibers. There is some evidence to indicate also that during the anaphase a pushing is exerted upon the retreating segments, yet this view can not be accepted without the greatest reserve, as the presence of a large bundle of fibers extending from each daughter segment to the poles argues strongly in favor of a pulling or contracting of the fibers.

According to the best cytological evidence the micro- and macrospore mother-cells are homologous. That type of development of the embryo-sac in which four potential macrospores

are produced as the result of the heterotypic and homotypic mitoses, occurring in gymnosperms as well as in the majority of angiosperms, is regarded as the more primitive, while that typified by Lilium is interpreted as a derived condition.

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*** In justice to the author it should be stated that the publication of the foregoing paper has been prevented for six months by unreasonable delay in the lithographing of the plates.—EDS.

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EXPLANATION OF PLATES XI–XIV.

All figures were drawn from sections with the aid of the Abbé camera lucida and with Zeiss apochromatic homogeneous immersion 2 mm., apert. 1.40, with compensating oculars 6 and 8, or with Leitz homogeneous immersion $\frac{1}{16}$ and oculars 1 and 3.

FIGS. 1–18. Pollen mother-cell of *Lilium Martagon*. *Figs. 1–11* refer to the first mitosis; *12–18* to the second.

FIG. 1. *a*, *b*, *c*, and *d* represent four chromosomes shortly after the cross segmentation of the spirem; in *a* the daughter segments are somewhat closely applied and twisted upon each other; in *b* the ends show a tendency to separate and diverge; and in *c* the segments are almost separate save at one end; *d* is a case in which the chromosome is somewhat bent and the segments are in close contact near the middle. × about 1750.

FIG. 2. Various forms of chromosomes observed in the nuclear plate: *a*, the chromosome is fastened to the spindle at the end, and consists of two rod-shaped segments twisted upon each; *b*, the two segments which adhere at both ends bend out at the middle to form the ring-shaped chromosome; such chromosomes are generally placed tangentially upon or within the spindle; *c* to *h* represent several other forms of chromosomes commonly met with; the bundle of fibers shows the method of attachment to the spindle; *f* is an X-shaped chromosome, although in this form of chromosome the ends may diverge more; *h* is a typical Y-shaped chromosome. *a* and *b*, × 1750; *c* to *h*, × 1500.

FIG. 3. A nearly mature spindle; the chromosomes are being arranged in the nuclear plate. × 1500.

FIG. 4. A mature spindle showing only three chromosomes. × 1500.

FIG. 5. Chromosomes in metakinesis; each daughter chromosome consists of two granddaughter segments as the result of the second longitudinal splitting; the granddaughter segments adhere at the ends to which the bundle of spindle fibers is fastened, while the opposite ends diverge to form the familiar V-shaped figures; the chromosomes in this figure are all fastened to the spindle by the ends. × 1500.

FIG. 6. Two chromosomes from a karyokinetic figure in the same stage as *fig. 5*; the chromosome at the right was fastened endwise to the spindle, and consequently the retreating pairs appear as two rods lying side by side or as V-like figures; the chromosome at the left was in the form of either a complete open or an incomplete ring: the daughter segments are therefore somewhat U- or V-shaped with one limb of the U, or V a little longer than the other; the V-shape here is due to a bending; each U or V is double as a result of the second longitudinal fission. × 1750.

FIG. 7. Median section of an entire pollen mother-cell. The chromosomes are in the anaphase; the granddaughter segments form V's or pairs of nearly parallel rods. × 1500.

FIG. 8. The same stage as the preceding; the daughter chromosomes on the right and left consist each of two U- or hook-shaped granddaughter segments owing this form to a bending; the granddaughter segments of those in the middle are contiguous rods slightly bent or hooked at one end. × 1500.

FIG. 9. Five daughter chromosomes nearly at the poles; the granddaughter segments which are at a slight distance apart are connected by fine threads. × 1750.

FIG. 10. The granddaughter segments are forming the spirem of the daughter nucleus by uniting end to end; between the daughter spirems extends the system of connecting fibers. × 1500.

FIG. 11. Daughter nucleus seen obliquely from the pole side; the spirem is arranged chiefly in long and regular turns. × 1750.

FIG. 12. A multipolar spindle of the second mitosis; the loops and turns of the partly segmented spirem are entangled; some of the free ends were made by the knife in sectioning; as a rule, at this stage the spirem is much more entangled and kinked, so that it is impossible to trace the individual pieces; the chromosomes are probably being pushed into the nuclear plate. × 1750.

FIG. 13. The spindle is bipolar, but the chromosomes are not completely oriented into the nuclear plate; it seems also that the spirem is not wholly segmented.

FIGS. 14, 15. The spindle is about mature, and the arrangement of the chromosomes is typical except that they are very often much more irregular, twisted, and kinked; in these two figures it is clearly seen that some of the segments of the chromosomes are twisted upon each other, while others are separate, lying tangentially (*fig. 14*) upon opposite sides of the equator. × 1750.

FIG. 16. Chromosomes in metakinesis; the separating elements are often variously bent or curved.

FIGS. 17, 18. Two spindles in anaphase; the retreating chromosomes are more or less curved or undulating rods which are almost invariably slightly hooked at the ends to which the fibers are attached.

FIGS. 19–29. Pollen mother-cell of *Podophyllum peltatum*. *Figs. 19–24* refer to the first, and *25–29* to the second division.

FIGS. 19, 20. Mature spindles; in *fig. 19* the chromosomes on the right and left are ring-shaped; in the central one the segments are in contact at only one end and each is curved; the picture presented by the nuclear plate of *fig. 20* is perhaps more frequent and typical; here also the chromosomes adhere at one end only; the segments are almost invariably curved, and the ends in contact are sometimes fused in such a way as to present a lump or swollen place. × 1500.

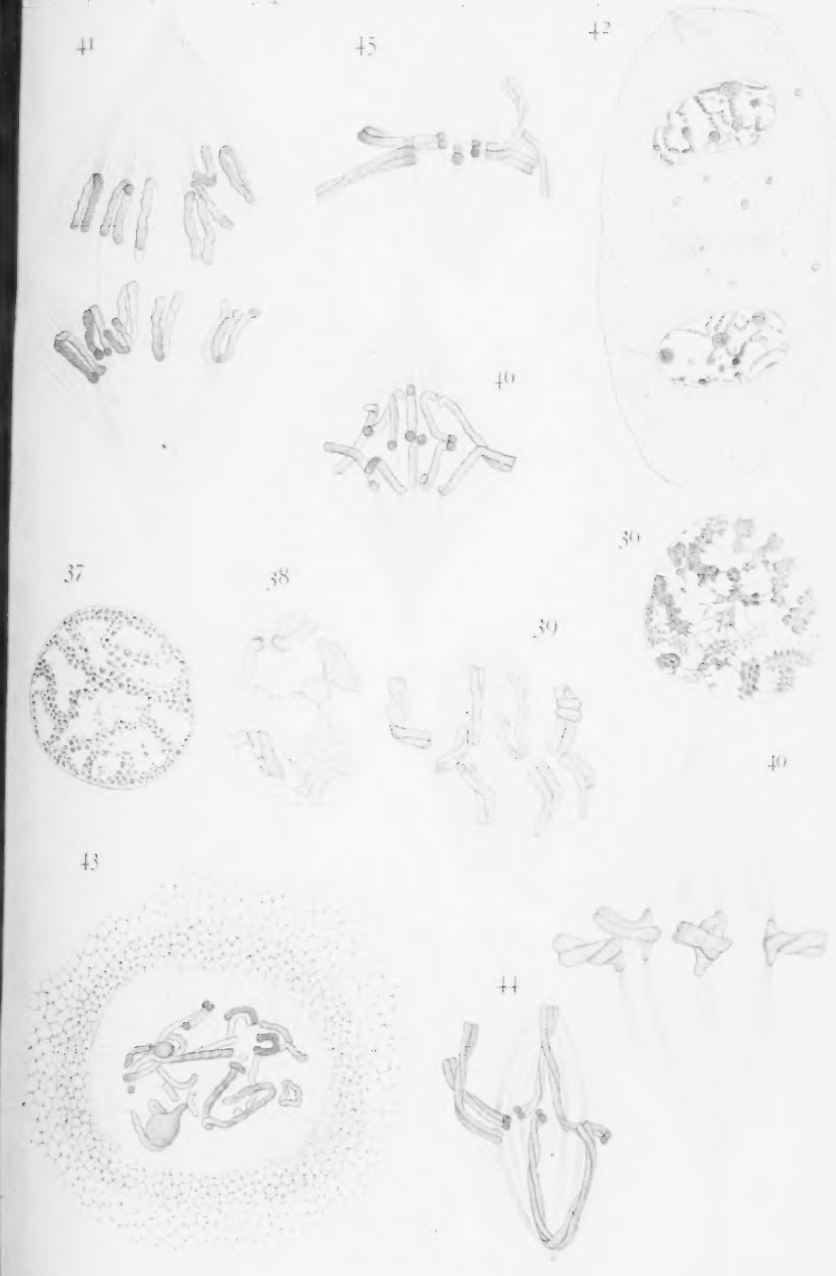
FIG. 21, *a* and *b*. Two chromosomes in metakinesis; the second longitudinal fission is plainly manifested; the chromosome *a* was oriented as in *fig. 20*; that at *b* was probably fastened to the spindle by one end, and stood radially to its axis; the retreating daughter chromosomes of *a* will be double U's, while those of *b* will probably give V's, or merely pairs of parallel and contiguous rods. × 1500.

FIGS. 22, 23. Two karyokinetic figures in anaphase; the two granddaughter segments of each daughter chromosome are clearly seen at this stage; they are either somewhat U-shaped, straight, or slightly curved rods. × 1250.

MOTTIER on CHROMOSOMES.

MOTTIER on CHROMOSOMES.

MOTTIER on CHROMOSOMES.



MOTTIER on CHROMOSOMES.

FIG. 24. Three chromosomes at a little later stage seen obliquely from the pole. × 1250.

FIG. 25. Daughter nucleus showing hollow spirem; the free ends indicate where the spirem was cut by the microtome knife.

FIG. 26. An entire pollen mother-cell showing the two multipolar spindles of the daughter nuclei. × 1750.

FIG. 27. A multipolar spindle of a daughter nucleus at a later stage than the preceding, in which fewer poles are present; the chromosomes are being arranged in the nuclear plate.

FIGS. 28, 29. Two mature spindles; although in *fig. 29* the segments of the chromosomes are not closely applied to each other, yet this is not a later stage than *fig. 28*.

FIGS. 30–39. *Tradescantia virginica.*

FIG. 30. Mature spindle; the points of the crescent-shaped daughter segments adhere to form ring-like chromosomes except in the one at the right; two of the chromosomes are fastened together by the fusion of one of the points of each crescent to one of the other; in the chromosome at the right only one point of the segments adhere. × 1250.

FIG. 31. The same stage as *fig. 30;* the daughter segments of the three chromosomes on the left are united only at one end; they are short, thick crescents with blunt ends, and when thus oriented they frequently reach almost from pole to pole. × 1250.

FIG. 32. The daughter segments have just separated; at this stage the second longitudinal fission is often not apparent. × 1250.

FIG. 33. The anaphase; at this stage it is evident that the daughter chromosomes have split lengthwise. × 1250.

FIG. 34. The same stage as *fig. 33;* the chromosomes are seen from the pole. × 1250.

FIG. 35. Daughter nucleus seen from the pole: the granddaughter segments of the twelve chromosomes show a tendency to become separated; their surfaces present an eroded appearance. × 1750.

FIG. 36. Daughter nucleus in which the chromosomes are much reticulated and the identity of the individuals cannot be definitely made out. × 1750.

FIG. 37. Daughter nucleus in which all identity of the chromosomes is lost. × 1750.

FIG. 38. The chromosomes are differentiated preparatory to the formation of the spindle. × 1750.

FIG. 39. Mature spindle of second mitosis; the chromosomes are longer and more regular than is usual. × 1750.

FIGS. 40–46. Embryo-sac of *Lilium Martagon.*

FIG. 40. Mature spindle of first karyokinesis in embryo-sac; the chromosomes stand radially upon the spindle. × 1500.

FIG. 41. The anaphase of the same division; the pairs of granddaughter segments are similar to those in the pollen mother-cells.

FIG. 42. Embryo-sac with two daughter nuclei which are nearly in the resting condition; the connecting fibers have not entirely disappeared; less highly magnified.

FIG. 43. An upper daughter nucleus in an early stage of spindle-formation; the nuclear membrane as such has disappeared, and numerous spindle fibers have penetrated the nuclear cavity; the chromatin spirem is not segmented; the free ends have been made by the knife. × 1500.

FIG. 44. Bipolar spindle of second division; the spirem does not seem completely segmented. × 1500.

FIG. 45. A mature spindle; the chromosomes are regularly oriented in the nuclear plate; the long, slender segments are contiguous and twisted upon each other. × 1500.

FIG. 46. The same in metakinesis. × 1500.

BRIEFER ARTICLES.

NOTES ON NORTH AMERICAN GRASSES.

III. NEW SPECIES OF WILLKOMMIA. (WITH TWO FIGURES.)

Willkommia texana Hitchc., n. sp.—A tufted perennial. Culms smooth, a foot or two high, erect from a decumbent base. Radical

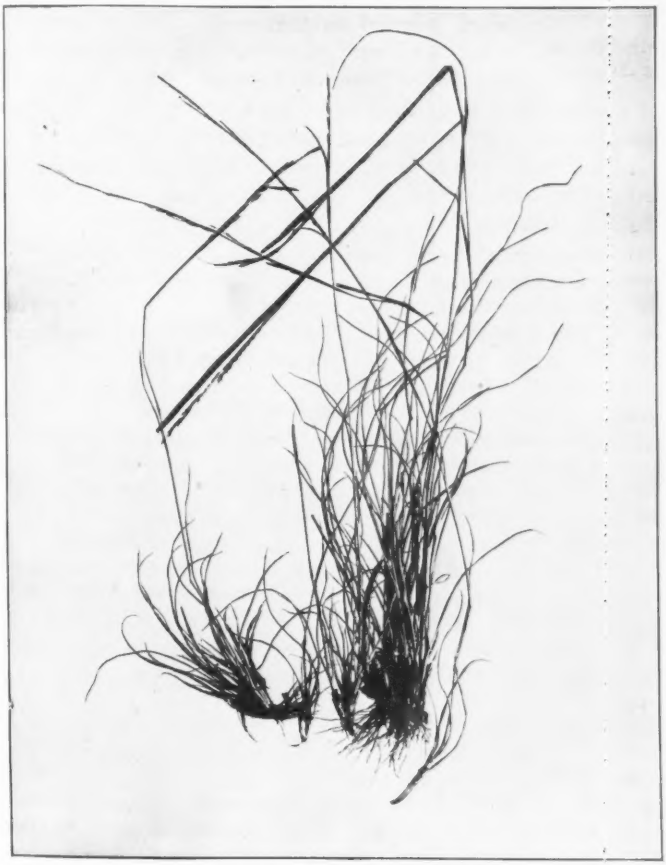


FIG. 1.—*Willkommia texana* Hitchc.

leaves several, 3 or 4 inches long, involute, tapering to a sharp point, upper surface rough, margin scabrous, otherwise smooth. Stem leaves few, the upper larger and embracing the lower part of the panicle. Inflorescence a panicle of spikes, a few inches to a foot long. Spikes several, an inch or two long, distributed along the axis. Spikelets several, arranged in two rows along one side of a flattened axis, 1-flowered, appressed. Empty glumes 2, 1-nerved, smooth, thin, and light colored, pointed but not awned, lower about half as long as upper, which is green on the margins. Flowering glume about the length of the upper empty glume, obtuse and awnless, 3-nerved, the lateral pair near the margin and densely ciliate with long white hairs, also pubescent between nerves. Palea nearly as long as flowering glume, 2-keeled, the nerves ciliate like the flowering glume. The base of the flower extends down into a short, hairy callus. Stamens 3. Caryopsis oblong, smooth, margined, and apiculate above.

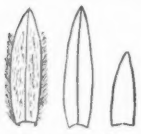


FIG. 2. — Details of flower.

DISTRIBUTION: Ennis and Beeville, Texas, *J. G. Smith*, 1897.

The specimens were found among the undetermined forms of Leptochloa in the Herbarium of the U. S. Department of Agriculture. The plant from Ennis may be considered the type. I have referred this species to Hackel's genus Willkommia as it agrees with the description in all essential particulars, and in generic characters with the specimen of *Willkommia annua* which is in the Department Herbarium. In floral characters it differs chiefly in the awnless flowering glume. The distribution of the genus is peculiar, as the three previously described species occur in west South Africa.

The genus Willkommia was described by Hackel, Verh. Bot. Ver. Brandenburg 30: 145. 1888. This name had already been applied to a group of Compositæ (Sch. Bip. ex Nym. Consp. 357. 1879), which is now generally referred to Senecio. Hackel was aware of this, but, from the fact that the earlier name was now a synonym, considered himself justified in taking up the same name for his new genus of grasses.

This genus is allied to *Schedonnardus* Steud. and *Craspedorachis* Benth., but is distinguished from the former by the broad, hyaline, unequal empty glumes and the densely ciliate flowering glume and palea, and from the latter by the unequal empty glumes and the flowering glume as long as the upper empty glumes. Craspedorhachis has equal empty glumes twice as long as the flowering glume and palea.

I am of the opinion that Willkommia should be referred to Craspedorhachis Benth. (Hook. Icon. Pl. III. 4: 58. *pl. 1377*. 1882), but as Hackel, who has had the opportunity of examining all the African species, has kept the two genera separate I have done the same.

Hackel describes a second species of Craspedorhachis, *C. Menyharthii*, Bull. Herb. Boiss. II. 1: 770. 1901, from southeast Africa, in which the flowering glume is only one-fourth to one-fifth shorter than the outer glumes, thus making the difference less between our plant and the genus Craspedorhachis.—A. S. HITCHCOCK, *Bureau of Plant Industry, U. S. Department of Agriculture.*

THE MORPHOLOGY OF SPORE-PRODUCING MEMBERS.

[In view of the fact that Professor Bower's last paper,[1] which contains the general conclusions from his studies of spore-producing members, is not likely to appear for some time, we venture to publish in advance the following abstract of the memoir, which was read before the Royal Society on February 12, 1903, and kindly communicated to us.—EDS.]

THIS concluding memoir contains a general discussion of the results acquired in the four previous parts of this series, and of their bearing on a theory of sterilization in the sporophyte. The attempt is made to build up the comparative morphology of the sporophyte from below, by the study of its simpler types; the higher and more specialized types are left out of account, except for occasional comparison. It is assumed for the purposes of the discussion that alternation of generations in the Archegoniatae is of the antithetic type, and that apogamy and apospory are abnormalities, not of primary origin.

After a brief allusion to facts of sterilization in the sporogonia of bryophytes the similar facts are summarized for the pteridophytes. It has been found that examples of sterilization of potentially sporogenous cells are common also in vascular plants, while occasionally cells which are normally sterile may develop spores. Hence it is concluded that spore-production in the archegoniate plants is not in all cases strictly limited to, or defined by, preordained formative cells, or cell-groups. A discussion of the archesporium follows, and though it is found that in all Pteridophyta the sporogenous tissue is ultimately referable to the segmentation of a superficial cell, or cells, still in them, and indeed in vascular plants at large, the segmentations which lead up to the formation of spore mother cells are not comparable in all cases; in fact, that there is no general law of segmentation underlying the existence of that cell or cells which a last analysis may mark out as the "archesporium"; nor do these ultimate parent cells give rise in all cases to cognate products. Therefore it is concluded that

[1] BOWER, F. O., Studies in the morphology of spore-producing members. No. V. General comparisons and conclusions.

the general application of a definite term to those ultimate parent cells which the analysis discloses has no scientific meaning, beyond the statement of the histogenic fact.

Further, it is shown that the tapetum is not a morphological constant, but varies both in occurrence and origin; that even the individuality of the sporangium is not always maintained. All that remains then as the fundamental conception of the sporangium in vascular plants is the spore mother cell or cells, and the tissue which covers them in, for such cells are always produced internally. The definition of the sporangium may then be given thus: "*Wherever we find in vascular plants a single spore mother cell, or connected group of them, or their products, this with its protective tissues constitutes the essential of an individual sporangium.*" From the point of view of a theory of sterilization such sporangia may, at least in the simplest cases, be regarded as islands of fertile tissue which have retained their spore-producing character, while the surrounding tissues have been diverted to other uses. It will be seen later how far this view will have to be modified in the more complex cases.

In a second section of the memoir the variations in number of sporangia in vascular plants are discussed; the methods of variation may be tabulated as follows, under the heads of progressive increase and decrease:

I. *Increase in number of sporangia.*—(*a*) By septation, with or without rounding off of the individual sporangia; (*b*) by formation of new sporangia, or of new spore-bearing organs, which may be in addition to or interpolated between those typically present; (*c*) by continued apical or intercalary growth of the parts bearing the sporangia; (*d*) by branching of the parts bearing the sporangia; (*e*) indirectly, by branchings in the non-sporangial region resulting in an increased number of sporangial shoots; this is closely related to (*c*) and (*d*).

II. *Decrease in number of sporangia.*—(*f*) By fusion of sporangia originally separate; (*g*) by abortion, partial or complete, of sporangia; (*h*) by reduction or arrest of apical or intercalary growth in parts bearing sporangia; (*i*) by fusion of parts which bear the sporangia or arrest of their branchings; (*j*) indirectly, by suppression of branchings in the non-sporangial region, resulting in decreased number of sporangial shoots; this is closely related to (*h*) and (*i*).

We are justified in assuming that (subject to the possibility of other factors having been operative of which we are yet unaware) the condition of any polysporangiate sporophyte as we see it is the result-

ant of modifications such as these, operative during its descent. The problem will, therefore, be in each case to assign its proper place in the history to any or each of these factors.

It is pointed out that in homosporous types, which are certainly the more primitive, the larger the number of spores the better the chance of survival, and hence, other things being equal, increasing numbers of spores and of sporangia may be anticipated; but in the heterosporous types reduction in number both of spores and of sporangia is frequent. The former will accordingly illustrate more faithfully than the heterosporous forms the story of the increase of complexity of spore-producing parts. The general method put in practice here is to regard homosporous forms as in the upgrade of their evolution, as regards their spore-producing organs, unless there is clear evidence to the contrary. The *onus probandi* lies rather with those who assume reduction to have taken place in them.

A summary of evidence of variation in number of sporangia by any of these methods is then given for the Lycopodineae, Psilotaceae, Sphenophylleae, Ophioglossaceae, Equisetineae, and Filicineae; followed in each case by a theoretical discussion of the bearing of that evidence on the morphology of the spore-producing members. The general result is that all of them, including even the dorsiventral and megaphyllous types, are referable to modifications of a radial strobiloid type; progressive elaboration of spore-producing parts, followed by progressive sterilization, and especially by abortion of sporangia in them, of which there is frequent evidence, together with the acquirement of a dorsiventral structure, may be held to account for the origin of even the most complex forms. But the vegetative organs once formed may also undergo elaboration, and differentiation *pari passu* with the spore-producing organs, a point which has greatly complicated the problem, especially in the higher forms; all roots are probably of secondary origin; facts of interpolation of additional sporangia, especially in ferns, and of apogamy and apospory, are also disturbing influences which have probably been of relatively recent acquisition.

A comparison is drawn, as regards position, physiological and evolutionary, in the sporophyte, between the fertile zone in certain bryophytes and the fertile region of certain simple pteridophytes, *e. g.*, the lycopods; though no community of descent is assumed, the relation of the reproductive to the vegetative regions is the same. In the bryophytes that region is regarded as a residuum from progressive sterilization; it is suggested that the same is the case for a strobiloid

pteridophyte, such as Lycopodium. The theory of the strobilus, based on this comparison, is that similar causes would lead to the decentralization of the fertile tissue in the primitive pteridophytes as in the bryophytes, and result in the formation of a central sterile tract, with an archesporium, at its periphery; that such an archesporium, instead of remaining a concrete layer as it is in the larger Musci, became discrete in the lycopods; that the fertile cell-groups formed the centers of projecting sporangia, and that they were associated regularly with outgrowths, perhaps of correlative vegetative origin, which are the sporophylls.

Whether or not this hypothesis of the origin of a lycopod strobilus approaches the actual truth, comparison points out the genus Lycopodium as a primitive one, characterized by more definite numerical and topographical relation of the sporangia to the sporophylls than in any other type of Pteridophyta.

Then follows, as a consequence of comparison, the enunciation of a theory of the sporangiophore, a word which is here used in an extended sense to include not only the spore-producing organs of Psilotaceae, Sphenophylleae, Ophioglossaceae, Equisetaceae, but also the sori of ferns. The view is upheld that all these are simply placental growths, and not the result of "metamorphosis" of any parts or appendages of prior existence; that the vascular supply, which is not always present, is not an essential feature; that they are seated at points where in the ancestry spore-production has been proceeding on an advancing scale; hence they do not occupy any fixed and definite position. It seems probable that at least a plurality of sporangia existed on primitive sporangiophores, and that where only one exists that condition has been the result of reduction.

The above theories are then applied to the several types of Pteridophyta. The Lycopods, Psilotaceae, Sphenophylleae, and Ophioglossaceae may be arranged as illustrating the increased complexity of the spore-producing parts, and of the subtending sporophylls; the factors of the advance from the simple sporangium to the more complex sporangiophore are septation, upgrowth of the placenta with vascular supply into it, and branching, with apical growth also in the Ophioglossaceae. But even in the most complex forms, the sporangiophore may be regarded as a placental growth, and not the result of transformation of any other member.

In the case of Helminthostachys the marginal sporangiophores are regarded as amplifications from the sunken sporangia of the Ophio-

glossum type; in Equisetum they are regarded as being directly seated on the axis, and having originated there by a similar progression; they would thus be non-foliar. It is pointed out that though a foliar theory would be possible for Equisetum itself, it is not applicable to the facts known for the fossil Calamarieae, which are so naturally related to it. Thus the strobilus of the Equisetineae is of a rather different type from that of the Lycopods, Psilotaceae, or even the Ophioglossacae, in all of which there is a constant relation of the spore-producing parts to the leaves; in the Equisetineae no such constant relation exists; the leaves and sporangiophores may be in juxtaposition, as in Calamostachys, without exactly matching numerically; or the sporangiophores may occur in larger numbers and in several ranks, between suc cessive leaf-sheaths, as in Phyllotheca and Bornia; or without any leaves at all, as in Equisetum. Thus, on a non-phyllome theory the latter may be held to be only an extreme case of what is seen in certain fossils.

The ferns, notwithstanding their apparent divergence of character from other pteridophytes, may also be regarded as strobiloid forms, with greatly enlarged leaves; the primitive sori of the Simplices resemble the sporangiophores of other Pteridophyta; the more complicated soral conditions of the Gradatae and Mixtae were probably derivative from these, the chief difference being due to the interpolation of new sporangia, an innovation which is in accordance with biological probability, as well as with the palaeontological record.

The effect of the results thus obtained on the systematic grouping of the pteridophytes is then discussed; it is pointed out that the lycopods, Psilotaceae, Sphenophylleae, Ophioglossaceae, and Filices illustrate lines of elaboration of a radial strobiloid type, with increasing size of the leaf. The division of Pteridophyta by Jeffrey, on anatomical characters, into small-leaved Lycopsida, and large-leaved Pteropsida is quoted; but it is concluded that the anatomical distinction of Jeffrey does not define phylogenetically distinct races, but is rather a register of such leaf-development as differentiated them from some common source. It is contended that the Ophioglossaceae and Filices, which constitute Jeffrey's Pteropsida, are not necessarily akin on the ground of their large leaves, and consequent phyllosiphonic structure; but that they probably acquired the megaphyllous character along distinct lines. The opinion of Celakovsky is still held, "that the lycopods are probably of living plants the nearest prototypes of the Ophioglossaceae." The more recent investigations of Jeffrey and of Lang have shown, however,

that in the gametophyte of the Ophioglossaceae there is an assemblage of "filicinean" characters, which differ from those of Lycopodium itself. But Celakovsky's comparison is *with the lycopods, not with the genus Lycopodium;* so far as the facts go, increasing "filicinean" characters of the gametophyte follow in rough proportion to the larger size of the leaf; thus from Isoetes we learn that a combination of cross-characters is found in a megaphyllous lycopod type. What we find in the Ophioglossaceae is that in conjunction with their more pronounced megaphyllous form, still retaining, however, the lycopodinous type of the sporophyte, they show more pronounced "filicinean" characters of the gametophyte, and of the sexual organs. It is unfortunate that the facts relating to the gametophyte of the Psilotaceae and Sphenophylleae are not available in this comparison.

It is not obvious what the meaning is of this parallelism between leaf-size and characters of the sexual organs. A further difficulty in its interpretation lies in the fact that for the Equiseta the parallelism does not hold; there "filicinean" characters of the gametophyte accompany entirely non-filicinean characters of the sporophyte, the latter showing nearer analogy to the lycopods than to the ferns. Such cross-characters are difficult to harmonize with any phylogenetic theory; on account of them the Equisetineae are placed in an isolated position, and in the same way, though with less pressing grounds, a separate position should be accorded to those types which lie between the extremes of lycopods and ferns, in proportion as the characters are more or less pronounced.

On this basis the Isoetaceae would probably best take their place as a sub-series of the Lycopodiales, Ligulatae; the Psilotaceae and Sphenophylleae would constitute a series of Sphenophyllales, separate from, but related to, the Lycopodiales. The Ophioglossaceae would form an independent series of Ophioglossales more aloof than the latter from the Lycopodiales, but not included in the Filicales. The actual connection of these series by descent must remain open; it is quite possible that some or all of them may have originated along distinct lines from a general primitive group, which may be provisionally designated the Protopteridophyta; these were probably small-leaved strobiloid forms with radial type of construction, and with the sporangia disposed on some simple plan. The grouping arrived at in these memoirs may be tabulated as follows:

I. LYCOPODIALES.
  (*a*) Eligulatae.
    Lycopodiaceae.
  (*b*) Ligulatae.
    Selaginellaceae.
    Lepidodendraceae.
    Sigillariaceae.
    Isoetaceae.

II. SPHENOPHYLLALES.
    Psilotaceae.
    Sphenophyllaceae.

III. OPHIOGLOSSALES.
    Ophioglossaceae.

IV. FILICALES.
  (*a*) Simplices.
    Marattiaceae.
    Osmundaceae.
    Schizaeaceae.
    Gleicheniaceae.
    Matonineae.
  (*b*) Gradatae.
    Loxsomaceae.
    Hymenophyllaceae.
    Cyatheaceae.
    Dicksonieae.
    Dennstaedtiinae.
    Hydropterideae (?).
  (*c*) Mixtae.
    Davallieae.
    Lindsayeae.
    Pterideae, and other Polypodiaceae.

V. EQUISETALES.
    Equisetaceae.
    Calamarieae.

—F. O. BOWER, *University of Glasgow.*

CURRENT LITERATURE.

BOOK REVIEWS.

Influence of light and darkness.

THE RELATION of light to the growth and development of plants has been the subject of much study and experimental research for two centuries or more. Probably the largest contribution to the general knowledge of the subject, at least to the text-book literature, has been made by Sachs, aided by his pupils. He began publication in 1859, and exerted great influence in molding scientific opinion in this as in other parts of the science of plan ' physiology. As researches have multiplied and the subject has unfolded, the difficulty of making a satisfactory explanation of observed phenomena has increased.

A careful examination of the whole subject, coupled with observations upon a series of plants of wide relationship and diverse habits, has been much needed. A monographic work of this character has recently been published by Dr. D. T. MacDougal,[1] director of the laboratories of the New York Botanical Garden. It has been the aim of the author to secure ample facts with which to survey the whole field, and the substantial volume before us is evidence of success.

The work opens with a résumé of previous contributions, in which more than a hundred works are summarized in a lucid and critical manner. The author then records his own observations, giving an account of experiments on ninety-seven species of flowering plants, ferns and their allies, which have been grown in continual darkness, with control plants grown in light. The subjects were grown from tubers, corms, rhizomes, cuttings of leaves and stems, seeds, and spores. They represent aquatics, creepers, climbers, succulents, mycorhizal forms, geophilous and aerial shoots, mesophytes, and spiny xerophytes. The work has extended over a period of seven years, and embraces a wealth of data not readily apprehended without detailed examination. The great number of excellent original illustrations adds interest and value to the treatise.

A third of the volume is occupied with a discussion of the data, and their correlation with previous observations and conclusions. The matter is taken up from various points of view, and it is clearly shown that no theories heretofore propounded will apply to all cases. Although occasionally plants have acquired certain advantages through etiolation, the forms assumed in dark-

[1] MACDOUGAL, DANIEL TREMBLY, The influence of light and darkness upon growth and development. Memoirs of the New York Botanical Garden, II. Imp. 8vo. pp. 319, *figs.* 176. New York Botanical Garden. 1903. $2.00.

ness are not, as usually held, due to an effort on the part of the plant to reach the light. It is shown that the stimulating action of light may be transmitted through a considerable interval of both space and time, even affecting organs subsequently formed, so that conclusions drawn from so-called "partial etiolation" have frequently been erroneous. Often there is a direct action of darkness in producing morphological changes. It is well proven that in all cases a great difference exists in the morphological differentiation of tissues developed in darkness and in light, and in this discussion the distinction between growth and development is kept clearly in view. The author concludes that "none of the phenomena of etiolation or of diminished growth in light may be ascribed to the direct influence of light upon the tissues or cells concerned, but rather upon the organism as a whole."

It is, however, impossible to give in a brief review any adequate idea of the author's views upon the various aspects of the subject. He himself has tacitly admitted the futility of such an attempt by not providing a summary for the reader.

There can be no question of the great value of this contribution by Dr. MacDougal to a most important part of plant physiology. The vast array of carefully planned observations forms a substantial contribution in itself and the discussion brings the subject into a new and clearer light. An ample index both to the literature cited and to the text and illustrations completes the volume.—J. C. ARTHUR.

The heaths of northern Germany.

THE FIFTH volume of *Vegetation der Erde* differs from those that have preceded in that a single formation is dealt with, rather than a country or a natural phytogeographic subdivision. Graebner[2] has made the north German heaths a special study for a number of years, and in 1895 he published an extensive treatise on the subject, wherein many of his present results were anticipated. The close relationship between heaths and moors is clearly shown, and the impossibility of using the water content of the soil as the chief distribution factor is well brought out. Graebner makes a strong plea (as he has done in former papers) for a chemical classification of soils and plant formations. Adopting this idea, the heath belongs to the soil group which is poor in certain food materials, particularly potash, lime, and phosphoric acid. For chemical reasons, he believes that a heath soil can never develop a natural forest. The author's concept of the heath is rather broad, including not only areas dominated by ericaceous shrubs, but open tracts in which there is neither a good tree growth nor a close grass turf; ligneous plants dominate, especially low shrubs. What we call pine or oak barrens would probably be included in Graebner's heath. Moors or peat bogs also are difficult to delimit from the heath, many species, indeed, being common to both.

[2] GRAEBNER, P., Die Heide Norddeutschlands und die sich anschliessenden Formationen in biologischer Betrachtung. 8vo, pp. xii + 320. With map. Leipzig: Wilhelm Engelmann. 1901. Price *M* 21.50.

The most interesting of the chapters is the one which presents the dynamics of the heath formation. Graebner combats with great vigor the rather common view that heaths represent areas once forested, in which reforestation has been prevented directly or indirectly through the agency of man. He argues that most heath areas show no tendency to return to forests, when left quite free to do so, and that in many cases heaths even encroach upon forests. As already noted, the chemical nature of the soil is believed to be inimical to tree growth, and the *Ortstein* of the heath subsoil adds to the difficulty. The author departs from most commonly accepted views in regarding the climate as fundamentally responsible for the condition of these heathy soils. The most usual origin of the heath is from forests in which the soil has been made gradually poorer in necessary salts, partly by the trees themselves but more especially by leaching. The latter process is thought to be greater in northwestern than in northeastern Germany, because of greater rainfall. Hence the heath prevails westward under original soil conditions that bring forth forests eastward. The heath may originate on naked sand through a series of stages, the first of which is characterized largely by algae and moss protonemata. Graebner also shows how heath moors may originate, giving three cases: development from water, from naked soil, and from forests. The heath may develop from these moors, if for any reason they become dry. Sections are devoted to the soil species and climatic features of the heath region.

The second part of the book treats of the various types of heaths, which the author divides into four groups. (1) Heaths proper, including Calluna, Tetralix, Empetrum, and Sarothamnus heaths; (2) grass heaths, dominated by xerophytic grasses; (3) forest heaths, mostly dominated by pines; (4) Weingaertneria heaths. The final section deals with the relation of the heath to other formations. This volume is easily the most readable of those which have been thus far published, and it is to be hoped that other volumes which deal with definite formations will follow soon.— H. C. COWLES.

Vegetation pictures.

KARSTEN and SCHENCK[3] have inaugurated a valuable series of illustrations of the world's vegetation, of which two numbers have thus far appeared. Each number contains six excellent heliotypes, representing characteristic plant formations in various parts of the world. Full descriptive text accompanies each picture, so that reference to various original monographs is scarcely necessary. The first number, prepared by Schenck, deals with southern Brazil, presenting views of the tropical rainy forest, myrmecophilous trees, palms, epiphytes, and Araucaria woods. Karsten has given out the second number, which contains views from the Malay archipelago, presenting the Nipa formation, tree ferns, rainy forest and street

[3]KARSTEN, G., and SCHENCK, H., Vegetationsbilder. 4to. Jena: Gustav Fischer. 1903. Subskriptionspreis jedes Heft von 6 Tafeln *M* 2.50. Einzelne Hefte *M* 4.

scenes. The illustrations are usually well executed and will prove of great value in botanical classes.

The vegetation of east Africa, so long poorly known, but now so fully brought to light by the work of Dr. Engler and his associates, is presented yet more clearly by an excellent series of 64 reproductions from photographs, taken by Walther Goetze, who lost his life while engaged in this work.[4] Among the views here presented are coastal steppes, high grass steppes, Acacia and other tree steppes, palm woods, Euphorbia thickets, alluvial forests, mountain woods and thickets, mountain meadows, rainy forests, etc. Good text descriptions accompany the views, and it is safe to say that one may get from a careful study of this work a vivid and true picture of many of the plant formations of German East Africa.—H. C. COWLES.

MINOR NOTICES.

A. J. MCCLATCHIE[5] has brought together a large amount of interesting information concerning Eucalyptus. The purpose of the bulletin is to give information concerning the characteristics of the "eucalypts," their climatic requirements, and their uses; to give directions and suggestions as to their propagation and culture; and to furnish a means of identifying seedlings and mature trees. It seems that these trees now serve very many useful purposes in the Southwest, and give promise of great future usefulness in the semi-arid portions of our continent. The covering of the now untillable treeless portions of the semi-tropic section of America with such trees as eucalypts, which will yield fuel, timber, and other useful products, and also furnish protection from the sun, from winds, and from floods, or otherwise ameliorate existing climatic conditions, is certainly an achievement greatly to be desired. The characteristics of forty-one species, being the principal ones grown in America, are discussed, and illustrated by the ninety-one handsome reproductions of photographs.—J. M. C.

HILDEBRAND[6] has published under the title *Aehnlichkeiten im Pflanzenreich*, a volume rather out of the ordinary in the nature of its contents. The material presented is familiar to botanists, and yet would not particularly attract the popular reader. The stock cases of similarity in general habit, and in various organs (such as cacti and euphorbias, leaves and phylloclades, raspberries and mulberries, chestnuts and horse chestnuts) are mar-

[4] ENGLER and GOETZE, Vegetationsansichten aus Deutschostafrika inbesondere aus der Khutusteppe, dem Ulugurugebirge, Uhehe, dem Kingagebirge, vom Ruogwe, dem Kondeland und der Rukwasteppe, nach 64 von Walther Goetze auf der Nyassa-See und Kinga-Gebirgs-Expedition der Hermann und Elise geb. Heckmann Wentzel-Stiftung hergestellten photographischen Aufnahmen.

[5] MCCLATCHIE, A. J., Eucalypts cultivated in the United States. U. S. Dept. of Agric., Bureau of Forestry, Bull. 35. pp. 106. *pls.* 91. 1902.

[6] HILDEBRAND, F., Ueber Aehnlichkeiten im Pflanzenreich. 8vo. pp. iv+66 Leipzig: Wilhelm Engelmann. 1902. Price *M* 1.60.

shalled under different headings; a section is likewise devoted to similarities between plants and animals. The conclusions deal with causes and uses. Aside from genetic relationship and similar life conditions, the author thinks that hidden inner causes also cause similarities (e. g. in the pods of legumes and crucifers). The author thinks that likenesses, like many other things in plants, are generally useless, and that there is nothing analogous to the use of mimicry by animals.—H. C. COWLES.

M. LE PROFESSEUR ABBÉ H. LÉVEILLÉ[7] has begun the publication of an elaborate monograph of the genus Onothera, all of whose species are American, with the exception of a single Tasmanian species. This first fascicle comprises 138 pages, with numerous heliogravure plates and text cuts. After an analysis of Spach's monograph of 1835, and a general statement concerning anatomical characters and those from the seed the genus is presented under its five grand divisions (Scutiformes, Nuciformes, Laterniformes, Siliquiformes, and Prismatiformes). The species of each division are then presented and illustrated, the fascicle ending in the midst of the third group. The second fascicle is promised early in 1903, and the third in February 1904.—J. M. C.

H. VON SCHRENK[8] has published an account of a disease of the white ash caused by *Polyporus fraxinophilus*, which is very prevalent in the Mississippi valley, and is particularly severe in Missouri, Nebraska, and eastern Kansas, fully 90 per cent. of the trees in some localities being affected. The bulletin discusses the geographical distribution of the disease, susceptibility to this disease, method of attack, diseased wood, the sporophore, microscopic changes in the wood, growth of the fungus in dead wood, and remedies. —J. M. C.

THE LAMENTED DEATH of Dr. K. Gustav Limpricht is fortunately not to interfere with the completion of his work, *Die Laubmoose*, in Rabenhorst's *Kryptogamen-Flora*. The thirty-eighth part of the work, just issued, bringing the supplement well into the Bryums, and thus covering about three-fourths of the original, bears the name of Dr. W. Limpricht in association with his father's. Another part will probably close the final volume.—C. R. B.

O. VON SEEMEN[9] has published an admirable account of the willows of Japan. After a discussion of previous contributions, geographical distribution, and the general principles of classification in the group, the 33 species are presented, 8 of which are new. The descriptions are very full, and the plates leave nothing to be desired.—J. M. C.

[7] LÉVEILLÉ, H., Monographie du genre Onothera. Le Mans. 1902. Edition 200 copies, price 100 *fr.*

[8] VON SCHRENK, HERMANN, A disease of the white ash caused by *Polyporus fraxinophilus*. U. S. Dept. Agric., Bureau of Plant Industry, Bull. 32. pp. 20. *pls.* 5. Feb. 1903.

[9] SEEMEN, O. VON, Salices Japonicae. pp. vii + 83, *pls. 18*. Leipzig: Gebrüder Borntraeger. 1903. *M* 25.

LIEFERUNG 216 of Engler and Prantl's *Die natürlichen Pflanzenfamilien* is devoted to the conclusion of the treatment of the Orthotrichaceae, to a presentation of the Splachnaceae with 61 species, and of the Funariaceae except the last genus, Funaria. The mosses are now the only group incomplete in this monumental work.—C. R. B.

PROFESSOR ENGLER[10] has published a third edition of his very useful outline of the classification of plants. It will be remembered that this includes the characterization of all families and their important subdivisions; with special mention of useful plants, since the book is intended for the use of pharmaceutical students.—J. M. C.

NOTES FOR STUDENTS.

W. A. WHEELER[11] has published a list of the grasses of Minnesota, based mainly on his redeterminations of the material in the herbarium of the University of Minnesota. The list includes 178 species and varieties, 24 species not having been previously reported from the state.—J. M. C.

NĚMEC[12] reports that the action of benzol and 1 per cent. $CuSO_4$ on the roots of Pisum and Vicia causes many cells to contain two or more nuclei. A few hours later these nuclei are found to have reunited; this fusion of nuclei is obviously not in the least homologous with sexual fusion. The roots eventually die.—E. B. COPELAND.

MELVILLE T. COOK,[13] in investigating *Agrostemma Githago*, finds that the ovulate archesporium consists of one to three cells "of which all but one are absorbed," that a short beak projects through the micropyle, that two or three rows of cells "degenerate" to form a passage for the pollen-tube, that the proembryo is filamentous, later differentiating into a filamentous suspensor with vesicular basal cell and a large spherical embryo.—J. M. C.

CYRIL CROSSLAND[14] has suggested the way in which mangrove seedlings succeed in finding a lodgment on the coast of British and German East Africa, the whole of which is composed of a hard coral limestone. The peculiar seedlings float out to sea in regular fleets, the bud projecting from the water. Upon reaching shore the root-tip is inserted into any softness or crevice of the bottom by the falling tide, and the ripples causing the seedling

[10] ENGLER, A., Syllabus der Pflanzenfamilien. Edition 3. Berlin: Gebrüder Borntraeger. 1903. *M* 4.

[11] WHEELER, W. A., Catalog of Minnesota grasses. Minn. Bot. Studies 3: 83–107. 1903.

[12] NĚMEC, B., Ueber ungeschlechtliche Kernschmelzungen. Sitzber. Böhm. Gesells. Wiss. 1902. Repaged reprint, 6 pp.

[13] COOK, MELVILLE THURSTON, The development of the embryo-sac and embryo of *Agrostemma Githago*. Ohio Naturalist 3: 365–369, *pls.* 7–7*a*. 1903.

[14] CROSSLAND, CYRIL, Note on the dispersal of mangrove seedlings. Ann. Botany 17: 267–270. 1903.

to oscillate about the tip, it slowly bores down into any mud or crevice.—J. M. C.

W. C. WORSDELL,[15] using the theory that sporophylls preceded in time all other kinds of leaves, and that the latter have been gradually differentiated from the former by sterilization, has attempted to trace the origin of the flower from such a strobilus as that of the cycads. He calls attention to the fact that in this strobilus the lowest sporophylls are sterile, and claims that these are the progenitors of the floral leaves of angiosperms. He traces the line into the Ranunculaceae, through such forms as Myosurus, and presents a diagram illustrating the origin of calyx and corolla in the family.—J. M. C.

VERY FEW of the Rhodophyceae multiply vegetatively by brood organ or reproductive fragments such as are found in several other groups of thallophytes and among the bryophytes. Okamura,[16] however, reports a clear case in *Chondria crassicaulis* from Japan. Small knob-like branches are formed in the summer, which become richly stored with starch, and ripen in winter, when they are easily detached from the parent plant. Filamentous hold-fasts are developed at the proximal end which doubtless attach the structure when it drifts to a suitable resting place. This habit recalls that of certain Characeae whose nodal regions, stored with starch, may survive an unfavorable season and later produce new growths.—B. M. DAVIS.

MARLOTH[17] has secured some interesting results from a study of Roridula, one of the Droseraceae of South Africa, and the only shrubby member of the family. Roridula with its sticky "tentacles" catches insects to supplement its food-supply, but a spider robs the plant of a share of its prey, being able to walk or run over the leaves without the slightest hindrance from the sticky secretion of the tentacles. At the same time, a small hemipterous insect (capsid) feeds upon the juices of the plant, having likewise acquired immunity from the dangers of the glandular hairs; but the plant utilizes it, by certain attractions in the flower and specially developed mechanical contrivances, to effect cross-pollination.—J. M. C.

A CONTRIBUTION to proteid assimilation in molds is made by W. Butkewitsch,[18] working in the Leipzig laboratory. Aspergillus, Penicillium, and three species of Mucor were grown in solutions of Witt's peptone and of fibrin, and the effect upon the medium was carefully studied. In cultures

[15] WORSDELL, W. C., The origin of the perianth of flowers, with special reference to the Ranunculaceae. New Phytol. **2**: 42–48. *pl. 3*. 1903.

[16] Okamura, K., On the vegetative reproduction of *Chondria crassicaulis* Harv. Bot. Mag. Tokyo **17**: 1–5. 1903.

[17] MARLOTH, R., Some recent observations on the biology of Roridula. Ann. Botany **17**: 151–157. 1903.

[18] BUTKEWITSCH, W., Umwandlung der Eiwessstoffe durch die niederen Pilze im Zusammenhange mit Bedingungen ihrer Entwickelung. Jahrb. Wiss. Bot. **38**: 147–240. 1902.

of Aspergillus most of the modified proteid takes the form of ammonia, while in those of the other molds very little ammonia is produced, decomposition stopping with the amido-acids, especially tyrosin and leucin. The trypsin-like enzyme which produces the last-named bodies is found not only in the cells, but also diffuses out into the medium. Aspergillus possesses the power to break down amido-acids into ammonia, hence the difference between it and the other forms studied.— B. E. LIVINGSTON.

P. and H. SYDOW[19] have commenced a monographic study of the Uredinales which is expected to take three or four years for completion. The work is to appear in fascicles and the first volume is to be devoted to the genus Puccinia. The species of Puccinia are not arranged under their subgenera, Eupuccinia, Heteropuccinia, Brachypuccinia, etc., but according to the families of their phanerogamic hosts. The account has then the effect of a host index elaborated to include descriptions of the parasites. The reason given for this unusual procedure is the impossibility of assigning numerous imperfectly known species to the proper subgenus. One would think, however, that the authors had assumed equally great difficulties because of the confusion which must finally result as specific limits and nomenclature are shifted both among the hosts and parasites. It will be a very useful book, however, if it can be revised at suitable intervals.— B. M. DAVIS.

SOME INTERESTING OBSERVATIONS on the structure and development of young plants of Oedogonium have been recorded by Fritsch.[20] The large disklike holdfast, so characteristic of many species, is by no means universal. There are forms with a rhizoidal base and small point of attachment. Floating plants have a large saclike end which is frequently found in connection with an air bubble, apparently formed by the plant itself. The cap formed at the first cell division of the germinating zoospore is not generally thrown off, although some species have this characteristic habit. The brown deposit, frequently found at the base of young plants, consists of "ferric oxid or of some salt thereof." The colorless condition of Oedogonium filaments probably indicates gradual death of the plant and is not a resting condition, as described by Keller (Proc. Acad. Nat. Sci. Phila. 1901). The paper concludes with an account of abnormal zoospore formation, and some exceptional forms of sporelings.— B. M. DAVIS.

ITEMS OF TAXONOMIC INTEREST are as follows: F. HEYDRICH (Flora **92**: 97–101. *figs. 4.* 1903) has published a new genus (*Rudicularia*) of Valoniaceae from Japan.—H. and P. SYDOW (Ann. Mycologici **1**: 35–36. 1903) have established a new Mexican genus (*Asteroconium*) of Melanconiaceae

[19] SYDOW, P. and H., Monographia Uredinearum. Vol. I, fasc. 1 and 2. *pls. 23.* Leipzig: Gebrüder Borntraeger. 1902. Each *M* 12.

[20] FRITSCH, F. E., The structure and development of the young plants in Oedogonium. Annals of Botany **16**: 467–486. *figs. 3.* 1902.

found on leaves of Litsea.—P. A. DANGEARD (*idem* 61–64) has published a new genus (*Rhabdium*) of Chytridiaceae.—N. L. BRITTON (Torreya **3**: 23. 1903) has described a new species of Eleocharis (*E. Smallii*) from Pennsylvania.—F. E. CLEMENTS (Bull. Torr. Bot. Club **30**: 83–94. 1903) in describing new Ascomycetes from Colorado has published *Tichosporium*, *Psilothecium*, *Ophiogloea*, *Scytopezis*, and *Heteroplegma* as new genera.—C. H. PECK (*idem* 95–101) has published a new fungous genus (*Mitruliopsis*) related to Mitrula.—A. HOLLICK (*idem* 102–105) has described a new Magnolia and a new Ficus from the Cretaceous of Kansas.—W. W. ROWLEE (*idem* 106–108) has described a new pine (*P. recurvata*) from the Isle of Pines.—W. A. MURRILL (*idem* 109–120) in his second paper on the Polyporaceae of North America presents Pyropolyporus, recognizing 18 species, 10 of which are new.—C. S. SARGENT (*Rhodora* **5**: 52–66. 1903) has published 13 new species of Crataegus recently recognized in eastern Canada and New England.—B. L. ROBINSON (*Rhodora* **5**: 85–89. 1903) has shown that *Echinodorus parvulus* is not to be regarded as an Alisma.—M. L. FERNALD (*idem* 90–92) has described a new Bidens (*B. Eatoni*) from Massachusetts.—P. HENNINGS (Hedwigia Beibl. **42**: 22–24. *figs. 5*. 1903) has described a new genus (*Ruhlandiella*) of Rhizinaceae from Germany.—J. M. C.

RECENT TERATOLOGICAL LITERATURE.— In the American Florist **19**: 866, 1902, are two excellent figures of torsion in the stem of carnations.—DRUERY (Gard. Chron. **32**: 226–228. *figs. 77–78*. 1902) records a cristate variety of *Pteris aquilina* growing spontaneously, and illustrates it by two photographs. —FLOYD (Rhodora **4**: 244–245. 1902) notes the discovery of a cristate form of *Nephrodium marginale*, and since the variation seems to be permanent proposes *N. marginale* forma *Davenportii*. The fixation of cristation in ferns is well known.— BOWER (Ann. Botany **17**: 278–280. 1903) figures and describes an abnormal specimen of *Lycopodium rigidum* Gmel. in which a sporophyll of slightly greater width than the average subtends two sporangia of slightly unequal size, and calls attention to the rarity of such variations in the Lycopodiaceae.— RAYMONDAND (Rev. Sci. du Limouscin **10**: 370–373. *pl. 3*. 1902) describes and figures syncarpy in the bean (*Phaseolus vulgaris*), and discusses at considerable length the question of the terminology which should be employed in such cases. The paper might give the impression of greater value had the author mentioned at least two or three of about fifteen descriptions which have been published of syncarpy in this species.— BRITCHER (Bull. Maine Agric. Exp. Station no. 86. 1902) discusses variation in *Trillium grandiflorum* Salisb., giving many tables of measurements and six plates from photographs of normal and abnormal forms.— Under the title "Petiolate connation in *Trifolium pratense*" WHITE describes (Torreya **2**: 183–184. 1902) abnormal leaves of *T. pratense* consisting of five and six leaflets on unusually strong petioles, and concludes that the examples represent cases of connation rather than the production of supernumerary leaflets.— Fasciation in *Lilium Henryi* is figured and described by HENRY

Garden **62**: 284. 1902). From the ground the stalk is almost flat, reaching a width of eight and one half inches at the top, with a thickness of only a quarter of an inch. The total length of the inflorescence is twenty-one inches and the total height of the plant seven feet and five inches.—" L." (Meehan's Monthly **12**: 152. 1902) records a specimen of *Lilium superbum* with four rows of petals. Three of the stamens had been transformed and the other three had distorted anthers. The editor comments on the observation and refers to a case in the tiger lily.—TROTTIER (Bull. Soc. Bot. Italiana **1902**: 44–50. *fig.*), in addition to bringing together a number of examples of teratological phenomena which are to be attributed to parasitic influence, presents some miscellaneous observations, noting the occurrence of a hypertrophy or fasciation in the male catkin of *Alnus glutinosa* Gaertn., fasciation of the stem in *Chrysanthemum Leucanthemum* L., fasciation and some accompanying malformations in *Euphorbia Cyparissias* L., abnormal leaves in *Fagus silvatica* L., floral proliferation, stasimorphy, and fasciation in *Galega officinalis* L., fasciation in *Passiflora coerulea* L., torsion of the stem in *Ranunculus acer* L., and formation of foliar ascidia in *Ulmus campestris* L. —FOCKEU (Rev. Gén. Bot. **14**: 517–521. *figs. 61–63.* 1902) describes floral monstrosities in *Digitalis purpurea* L. The abnormal flowers occupy the terminal portion of the inflorescence and are divided by him into three classes according to complexity of structure. The malformation, he concludes, is due to the growing together of two or more flowers. Abnormalities in the flowers of this species are especially well known and it seems hardly probable that the paper contains any forms which have not been noted in the very numerous papers, about twenty-five in number, which have touched on this point. It is unfortunate that some of the literature was not available to Fockeu.—CUSHMAN has recently published a paper (Amer. Nat. **36**: 865–885. *pls. 1–5.* 1902) in which he discusses and figures some of the abnormal forms of leaves in the adult plants and compares them with the seedlings of the following species: *Viola pedata* L., *Chelidonium majus* L., *Ranunculus acris* L., *Spiraea salicifolia* L., *Tanacetum vulgare* L., *Viola tricolor* L., and *Rosa rubiginosa* L. He assumes that these "localized stages" represent the form of ancestral types, and that with a knowledge of seedlings and ancestral forms, these "localized stages" may be used to great advantage in determining the phylogeny and relationships of the plant. As to whether deviations from the normal structure of the kind described in the present paper belong to teratology or not depends, very evidently, upon the way in which this very differently defined term is limited.—A paper of a type which is rare in these days, since it is an extensive paper on the abnormalities of plants, and of a type which is rare in the literature of teratology, in that it is a monographic treatment of a definitely limited field, is that of STENZEL (Bibliotheca Botanica **55**: 1–136. *pls. 1–6.* 1902). In an introduction of twenty-eight quarto pages, the first section is devoted to a consideration of the value of the deviations from the normal structure. In this section he reviews the

widely differing opinions which have been held since the time of Goethe, and illustrates the present and past valuation of teratological observations as data for morphological conclusions by a review of the work which has been done in the Abietineae. Here he admits freely the importance of embryogeny in the solution of questions in morphology, but also calls attention to some of the conclusions which have been reached by the recognized leaders in embryology, and suggests that it would be interesting to compare, both as to number and importance, the erroneous conclusions which have been drawn from embryological evidence with those which are to be attributed to the "Irrwege der Missbildungslogik." He expresses his own belief in the value of teratological evidence in the solution of morphological questions. Over one hundred pages are then devoted to the floral abnormalities, arranged according to the nature of the malformation, which have been observed in native orchids growing in the open. A discussion of the different types of abnormalities observed is not possible in this place, and of their value only the specialist can judge, but the mass of observations and references to literature will surely be of great value. The paper is illustrated by six lithographic plates.—J. ARTHUR HARRIS.

NEWS.

HENRY HOLT AND COMPANY announce that "a plant physiology," by Professor George J. Pierce, will be issued in the spring.

M. G. ROUY has begun the publication of a monthly *Revue de Botanique Systématique et de Géographie Botanique*, to be edited by himself.

PROFESSOR L. H. BAILEY has been appointed director of the college of agriculture and dean of the faculty of agriculture of Cornell University.

M. MILLARDET, formerly professor of botany at Bordeaux, who did much to restore the French vineyards after their destruction by phylloxera, died December 15 at the age of 64.

WE learn from *Science* that at Barnard College, Columbia University, Dr. H. M. Richards and Miss Margaret E. Maltby have been promoted to adjunct professorships of botany.

DR. G. R. WIELAND, of the Yale University Museum, has received a grant of $1,500 from the Carnegie Institution for the continuation of his researches on the structure of fossil cycads.

DR. J. B. OVERTON, professor of biology in Illinois College, has been appointed research assistant by the Carnegie Institution, and will spend a year at the Botanical Institute of the University of Bonn, at the instance of Professor Strasburger, to carry on researches under his direction.

THE FIRST CIRCULAR in reference to the International Botanical Congress to be held in Vienna in 1905 has been issued. It contains a complete list of the Committee of Organization, and also announces that the congress will be held June 12–18, 1905. All correspondence in reference to it should be addressed to Dr. A. Zahlbruckner, Vienna, I., Burgring 7.

DR. FREDERICK D. HEALD has been elected adjunct professor of plant physiology and general bacteriology in the University of Nebraska. He is to develop the work, begun last year, in general bacteriology, and to oversee the laboratory work in plant physiology. Dr. Heald is to begin his new work in the summer, taking charge of the classes in botany in the summer session.

ERRATA.—In the article by Professor Bruce Fink in the March number the editors are responsible for the transposition of the cuts on pages 203 and 205. The inapplicability of the legends will render the mistake obvious. The author wishes to repair his failure by now making grateful acknowledgment of his indebtedness to Mr. C. J. Hibbard, of Minneapolis, for the photographs from which illustrations were made.

THE OHIO State University has organized a lake laboratory, located at Sandusky Bay. A new building capable of accommodating 100 students and investigators will be erected in time for the summer session, which commences June 29 and closes August 7. The laboratory will be open longer to those who desire to continue their work. Twenty-four were enrolled last summer. The location offers varied conditions of open lake, bay, marsh, river, native forest, sandy beach, and rocky islands. The laboratory is supplied with boats, dredges, seines, etc. The extensive fishing industry of Sandusky, and the U. S. Fish Hatchery at Put-in-Bay give additional advantages. The botanical staff includes Professor W. A. Kellerman, Columbus, Ohio (to whom inquiries may be addressed), Professor J. H. Schaffner, and Mr. E. O. Jennings.

THE SIXTEENTH SESSION of the *Marine Biological Laboratory* at Woods Hole will extend from July 1 to August 12, 1903. The botanical staff, headed by Professor Bradley M. Davis, comprises nine members, representing seven institutions. There will be given an instructional course of lectures on thallophytes, with laboratory work; a course on general physiology for investigators; a series on plant hybridization and breeding; and a series of general lectures by members of the staff, investigators, and guests. The advantages of Woods Hole for botanical study are too well known to need restatement. The Carnegie Institution controls a number of research tables, which will be assigned to suitable applicants, and the laboratory provides others. All are free of expense. Information may be obtained from Professor B. M. Davis, The University of Chicago.

THE MICHIGAN Academy of Science met at Ann Arbor, March 26–28. Professor F. C. Newcombe was vice-president of the section of botany, whose program was as follows: The effect of dilute and concentrated sea water on Cladophora, S. O. MAST; The osmotic relations of algae to their environment, HOWARD S. REED; Protoplasmic movement in *Elodea canadensis*, RENA B. RAYMOND; Structural variations of Chara, ELLEN B. BACH; The latent period in traumatropism, GEORGE P. BURNS; Extent of the sensory zone for heliotropism of terrestrial roots, DARRELL H. DAVIS; Final demonstrations of thigmotropism in terrestrial roots, FREDERICK C. NEWCOMBE; On the absorption of water by foliage leaves, including a history of the subject, J. B. DANDENO; Notes on Michigan fungi, including some new species of Hymenomycetes, B. O. LONGYEAR; The lichen genus Physcia, E. E. BOGUE; Some interesting hybrid oaks in the vicinity of Ann Arbor, CHARLES A. DAVIS; Preliminary account of the distribution of *Quercus imbricaria* in Washtenaw County, CHARLES A. DAVIS; The geographic distribution of bog plants, E. N. TRANSEAU; The succession of plant societies in Ypsilanti and Augusta townships of Washtenaw county, FOREST B. H. BROWN; The new Michigan oak, *Quercus Alexanderi* Britt.; its characteristics and distribution, S. ALEXANDER.